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**GEOGRAPHIC VARIATION
AND THE SPECIES
PROBLEM IN THE SHORE-BIRD
GENUS LIMNODROMUS**

**BY
FRANK A. PITELKA**

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GEOGRAPHIC VARIATION AND THE SPECIES PROBLEM IN THE SHORE-BIRD GENUS LIMNODROMUS

BY

FRANK A. PITELKA

(Contribution from the Museum of Vertebrate Zoology of the University of California)

INTRODUCTION

EVIDENCE on morphological and ecological discontinuities between closely related species and on variational trends forecasting discontinuities within species now constitutes, for higher vertebrates at least, the best data we have on the course of adaptation and species formation. This will obviously continue to be true for some time to come. Intensive studies of species groups, of which there are relatively few for American birds, have provided much of the basic information we now have, and more are needed. At the same time that such studies elucidate species relationships, they serve to localize areas where critical problems of species ecology can be investigated and where available data on historical geology can be brought to bear on questions of phylogenetic history. Thus, detailed analyses of morphological variation and distributional relations in these species groups serve not only to provide a picture of evolutionary radiation in them, but simultaneously to orient us with reference to basic questions of ecology and faunistics.

These comments apply with special force to such a species group as the American shore birds of the genus *Limnodromus* (family Scolopacidae), the dowitchers. The relationships of the several recognizable forms in this group have long puzzled avian taxonomists. The dowitchers are snipelike birds that frequent shores and pond margins, both marine and fresh-water. They breed from Alaska eastward across Canada to the Ungava Peninsula and winter from the southern United States south to northern South America. Four recognizable, allopatric forms occur. An Asiatic species, *Pseudoscolopax semipalmatus* (Blyth), is placed in the genus *Limnodromus* by Peters (1934: 272) and others; but for reasons presented elsewhere (Pitelka, 1948) this species is not now considered to belong there. In other words, four known forms comprise the genus *Limnodromus*, *sensu stricto*, which is without demonstrated close relatives.

In *Limnodromus* there have been differentiated a relatively long-billed, long-legged, short-winged form, *L. scolopaceus*, and a short-billed, short-legged, long-winged form, *L. griseus*, represented by three races (*griseus*, *hendersoni*, and *caurinus*). *L. scolopaceus* breeds in northern and western Alaska, *L. g. caurinus* in southern Alaska, *L. g. hendersoni* in interior Canada, and *L. g. griseus* probably in Ungava. Two grades of divergence are clearly evident, a primary one between the long-billed and short-billed forms and a secondary one expressing itself as a major cline in the three transcontinentally distributed races of the short-billed form. It is evident from the nomenclature introduced here that, allopatric ranges and certain morphological similarities

notwithstanding, *scolopaceus* is considered to represent a full species. The basis for this conclusion, which must be a tentative one, is developed in subsequent sections.

For a review of the recent literature on the taxonomy of dowitchers the reader is referred to the Appendix (p. 63). But he should know that two strongly divergent views exist regarding, among other considerations, the specific status of *scolopaceus*. A number of separate problems enter into these two views, and a brief résumé of them here will help to indicate the need for the close examination of morphological and distributional details in the text which follows. This divergence of views attests to the interest that dowitchers have for students of geographic variation.

The first and majority point of view maintains that the Alaskan form, *scolopaceus*, is merely a race of *L. griseus* of interior Canada, and that no additional forms can be recognized. The second accords *scolopaceus* specific rank and recognizes two races of the short-billed dowitchers, *L. g. hendersoni* of interior Canada and *L. g. griseus* of eastern Canada.

There are several reasons for these differences in taxonomic interpretation. First, conclusive evidence that *L. griseus* breeds in eastern Canada is lacking, and some authors have emphatically doubted that the species breeds east of Hudson Bay. Taverner (1935), however, regards the Ungava Peninsula as the "greatest *terra incognita*" on the North American continent, and he states that the failure of ornithologists to find the short-billed dowitcher breeding there means little or nothing. Circumstantial evidence indicates that it does breed there.

The second reason for the differences is that collections of specimens previously studied have been numerically inadequate and statistical methods have not been applied. Also, dowitchers heretofore have not been examined for possibly significant age-group distinctions between adults and first-year birds. They are one group in the well-known North American avifauna in which the crude, impressionistic methods used in avian taxonomy in past years and even today have confused more than clarified basic relationships.

Third, all specimens from Alaska and the Pacific coast of Canada have, with few exceptions, been called *scolopaceus*. Actually, both short-billed and long-billed dowitchers occur in Alaska and are confused under the name *scolopaceus*. This has led to incorrect understanding of the characters of *scolopaceus*, *sensu stricto*, which in turn has led a number of students to question the validity of the inland race of the short-billed dowitcher, *hendersoni*. The known breeding range of *scolopaceus* is northern and western Alaska; that there is a southern Alaskan breeding population, herein shown to be that of the short-billed dowitcher, has been established only recently by Hurley (1932:17) and Shortt (1939:15).

Fourth, further confusion has resulted because, from the 1850's to the present, Atlantic coast records of a form larger than *L. g. griseus*, with buffy under parts and reduced ventral spotting, have been assigned to *scolopaceus* when actually they represent the inland race, *L. g. hendersoni*. Again it is clear that the characters of the long-billed dowitcher have not been correctly understood.

This study of the dowitchers is undertaken, then, with several purposes in mind: to provide a sound basis for the recognition of races and species and for the allocation of verifiable distributional records; to describe some of the evident trends of evolutionary differentiation, with special concern for distinctions to be made between closely similar species; to provide a preliminary interpretation of the distributional pattern in *Limnodromus* in the light of the known geologic history of North America; and to survey critically the taxonomic history of the several forms, which, for reasons given above, is a matter of extraordinary importance in this group.

ACKNOWLEDGMENTS

This study owes its origin to the perspicacity and efforts of the veteran bird collector Rollo H. Beck, of Planada, California. In the fall of 1945, Mr. Beck brought to the Museum of Vertebrate Zoology a valuable and critical sample of 311 dowitchers obtained in the previous four years in Merced County, in the San Joaquin Valley, California. Mr. Beck's collection of this series was stimulated by his observation that specimens which he had collected there earlier did not bear out Orr's (1940:63) conclusion that in California the short-billed dowitcher is five times more common than the long-billed form. My examination of the series from Merced County confirmed Beck's observation, as all 311 specimens proved to represent *scolopaceus*. For discussions of this problem see pages 11 and 18.

Throughout the course of this study many institutions and persons have generously permitted me to examine or borrow specimens in their care: American Museum of Natural History, including the L. C. Sanford Collection (through J. T. Zimmer and D. Amadon), British Columbia Provincial Museum (through G. C. Carl), California Academy of Sciences (through R. T. Orr and Grace Crowe), Carnegie Museum (through W. E. C. Todd), Charleston Museum (through E. B. Chamberlain), Chicago Natural History Museum (through E. R. Blake), Colorado Museum of Natural History (through A. M. Bailey), Dickey Collections, University of California at Los Angeles (through A. J. van Rossem), Fish and Wildlife Service, Washington, D.C. (through J. W. Aldrich), Los Angeles Museum (through K. E. Stager), Museum of Comparative Zoology, Harvard University (through J. L. Peters), Museum of Zoology of the University of Michigan (through J. Van Tyne), National Museum of Canada (through A. L. Rand and W. Earl Godfrey), Natural History Museum at Stanford University (through G. S. Myers), Academy of Natural Sciences of Philadelphia (through R. M. de Schauensee), Royal Ontario Museum of Zoology (through L. L. Snyder), San Diego Museum of Natural History (through L. M. Huey), United States National Museum (through H. Friedmann), University of British Columbia (through I. McT. Cowan), and the University of Utah (through W. H. Behle). Additional specimens were examined from the private collections of R. H. Beck, H. B. Conover, the late Ralph Ellis, I. M. Gabrielson, A. O. Gross, the late J. E. Law, the late T. T. McCabe, the late M. M. Peet, K. E. Racey, A. M.

Sprunt, Jr., I. R. Tomkins, R. W. Tufts, W. E. Unglish, and J. D. Webster. By granting a special permit the California Division of Fish and Game made possible the collection of the significant series of specimens obtained by Beck in the San Joaquin Valley as well as additional specimens from other parts of California.

To all the institutions and persons named above I express acknowledgment for valuable aid and friendly coöperation. I am indebted also to Alden H. Miller for helpful counsel in the course of this study, and to Seth B. Benson, D. Bernard Bull, Herbert Friedmann, W. Earl Godfrey, Joseph Hickey, C. E. Hope, J. R. Macdonald, J. L. Peters, Alexander Sprunt, Jr., J. Van Tyne, and J. T. Zimmer, all of whom provided items of critical information. Lois C. Taylor and Dorothy R. Pitelka assisted in the collecting of data. V. G. Duran took the photographs of specimens used in this paper.

MATERIALS AND MEASUREMENTS

In the course of this study, 2,908¹ specimens of *Limnodromus griseus* and *L. scolopaceus* have been examined. Because dowitchers nest in Arctic and sub-Arctic areas, the numbers of specimens from breeding areas are relatively small, approximately 15 per cent of the total. However, they are actually large enough to permit statistical treatment.

The total includes an especially large number (1,022) of specimens from California alone, almost all with competently collected field data. Reliable, detailed data are available on local geography and ecological conditions, both in the literature and from the author's acquaintance with many parts of the state. For these reasons the main text of this paper begins with an analysis of populations of dowitchers in California, where they occur as migrants and winter residents.

Information from California on local distribution and behavior of dowitchers has been supplemented by observations made by the author on several field trips in the San Francisco Bay region in the fall of 1946. Other field data used herein were obtained by Mr. Rollo H. Beck in coastal and interior parts of central California.

The following linear measurements were taken from skins: (1) wing, the chord; (2) length of bill, from upper basal margin of the culmen on the forehead to tip; (3) tarsus, from joint between tibiotarsus and tarsometatarsus behind to the distal margin of the scute covering the central articular prominence (trochlea). Available records of weights are summarized in table 9 (p. 17).

¹ Critical specimens are referred to in text and tables by use of the following symbols: AB, Allan Brooks collection, now in the Museum of Vertebrate Zoölogy; AM, American Museum of Natural History; BS, Fish and Wildlife Service collection (formerly Biological Survey); C, Carnegie Museum; OAS, California Academy of Sciences; CM, Chicago Museum of Natural History (formerly Field Museum); DC, Dickey Collections, University of California at Los Angeles; HBC, H. B. Conover collection, Chicago Museum; JEL, J. E. Law collection; KB, K. E. Racey collection; LCS, L. C. Sanford collection, American Museum; MCZ, Museum of Comparative Zoology; MVZ, Museum of Vertebrate Zoölogy; NMC, National Museum of Canada; PA, Academy of Natural Sciences of Philadelphia; ROM, Royal Ontario Museum of Zoology; US, United States National Museum.

PLUMAGES, MOLT, AND AGE GROUPS

Sound comparisons and statistical analyses of variability in any group of birds rest on a clear understanding of plumage sequence and age categories. In the following discussion, plumage characters useful in segregating first-year and adult birds are examined. Facts concerning molt are given only so far as they are relevant to this problem.

Summer plumages of dowitchers are black dorsally, variegated with brown and buff markings, and brown ventrally with varying amounts of spotting anteriorly and varying amounts of white posteriorly (see pls. 1-5). Winter plumages are gray dorsally and white ventrally with varying amounts of gray anteriorly on the upper breast and neck (see pls. 6 and 7). Juvenal plumages are distinct from either of these: the dorsum is dark brown patterned with buff; the venter is washed with dull gray and buff, more or less speckled anteriorly, and dull white posteriorly (see pls. 8 and 9).

The molt program in *Limnodromus* is briefly as follows: Postjuvenal and prenuptial molts are incomplete. The first summer plumage is followed by a complete molt, which then alternates annually with a partial prenuptial molt. If any juvenal feathers are retained into the first summer, summer as well as winter plumages are divisible into first-year and adult classes; counting in, then, the juvenal plumage, first-year birds occur in three plumages. But first-year plumages may so resemble adult plumages that the two cannot be separated, and it remains to be seen to what degree the plumage sequence in *Limnodromus* permits such separation. Although the main features of plumage sequence in dowitchers have been described by Bent (1927:119) and Witherby *et al.* (1940:212), certain details critical to correct segregation of age groups are either overlooked or erroneously recorded.

In *scolopaceus*, the rectrices, upper tail coverts, not just "some" innermost secondaries (Witherby, *loc. cit.*), but all the remiges except possibly some of the innermost secondaries, and some juvenal scapulars are retained through the postjuvenal molt. All these series undergo replacement during the complete postnuptial molt. The central juvenal tail feathers are more acuminate than those of the adult; they are tipped with buff, some buff occurring as well near the tips of the more lateral rectrices and on the white bars; the bars are not so sharply demarcated as in the adult, the buff near the tips often blending into a fuzzy bar margin; the dark bars are also more brownish, and in a worn condition become faded to a dull brown, the white areas wearing more rapidly than the brown areas.

It is important to emphasize that what has just been said applies to the long-billed form, *scolopaceus*. The postjuvenal molt in *scolopaceus* is not so protracted as is maintained by Bent (1927:119) and Witherby (1940:213); apparently the variation in extent of the partial postjuvenal molt has in part led them to believe that certain winter-taken specimens of mixed plumage were undergoing molt. The typical retention of all rectrices and most if not all upper tail coverts through the postjuvenal molt in *scolopaceus* is also not mentioned by Bent.

But the main difficulty is the assumption made by Bent (1927:110) that the "plumages and molts . . . are the same in both forms," long-bill and short-bill. Available accounts of the postjuvenal molt are correct when checked by study of specimens of the short-billed races. In these, the postjuvenal molt is evidently more extensive than in *scolopaceus*, since at least the rectrices and upper tail coverts are included. Replacement of rectrices, to which special attention was given in this study, and probably of other feather series, also, continues for some time after the postjuvenal molt is completed in *scolopaceus*. Rate of this replacement apparently varies considerably among individuals of *L. griseus*, but it is almost always completed in January or February.

It is evident, then, that feather series retained through the postjuvenal molt but replaced in all subsequent, postnuptial molts serve to distinguish the first-winter plumage from the adult plumage in both *L. scolopaceus* and *L. griseus*. Between them, at least two important differences occur in the postjuvenal molt: replacement of rectrices in *griseus*, their retention in *scolopaceus*; and protraction of at least the tail molt in *griseus*, no evidence for such molt protraction in *scolopaceus*.

The first summer plumage was not identified by Witherby *et al.* (1940:213), and Bent's (1927:119) remarks with respect to it present an inadequate picture, again in part because differences between the long-billed and short-billed forms were not recognized. The prenuptial molt producing the summer plumage includes almost the entire body plumage, some wing coverts, most of the scapulars, some of the tertials, and usually the middle pair of rectrices. Upper tail coverts are replaced to a variable extent in the prenuptial molt of first-year as well as of adult birds, and the new feathers are easily recognized by their pinkish cinnamon rather than white bars. These general statements apply to both first-year birds and adults and to both *scolopaceus* and the short-billed races. But certain differences in summer plumage between first-year and adult birds do occur; these are the presence, in the former species, of juvenal feathers which include lateral rectrices, remiges, some of the wing coverts, and even a few very worn tertials, or scapulars, or upper tail coverts. The sum of these observations is that in both *griseus* and *scolopaceus* the summer plumages of first-year and adult birds are distinct. Whether or not they can always be distinguished for practical purposes is another consideration, because by late spring the feathers of the winter plumage retained through the prenuptial molt are worn to a varying degree, and juvenal feathers are distinguished from adult with increasing difficulty as the season advances.

Among the juvenal feathers retained by the first-year birds, only the characters of the rectrices have proved distinctive enough to permit segregation of first-year and adult birds. These have been described above. It has also been pointed out above that only in *scolopaceus* are the juvenal rectrices retained through the postjuvenal molt. In *griseus*, replacement of these feathers usually occurs during the protracted postjuvenal molt, and it is not possible to distinguish the rectrices so acquired by the first-year bird and those of adults. Spring-taken specimens with primary tips, upper tail coverts, central rectrices of the first-winter plumage, and scattered, dull, apparently faded

juvenal tertials that are all worn to an appreciable degree may safely be classed as first-year birds, but these criteria do not serve to segregate all first-year birds, owing to the varying amount and extent of wear.

Another complication arises from the variability of the first prenuptial molt. Among individuals that undergo only partial migration or remain on wintering grounds during the first summer this molt may be partial, so that a mixed body plumage is produced. Occasionally the first prenuptial molt is omitted. Bent (*loc. cit.*) regards birds in mixed plumage as the only ones of the first-year age group, whereas actually the majority of them undergo as complete a prenuptial molt as do adults. This is easily proved in *scolopaceus* by segregation of birds in breeding plumage into two categories based on presence or absence of juvenal lateral rectrices. This character, together with that of worn primary tips and extremely worn juvenal upper tail coverts, serves to identify a first-year bird in otherwise adult summer plumage.

Replacement of rectrices in the prenuptial molt generally involves only the central pair (Rowan, 1932:18). In *scolopaceus*, in both first-year and adult classes, none may be replaced; if replacement occurs in first-year birds, more than the central pair may be replaced, although never all, and in adults only the central pair is replaced. Retention of all rectrices is more common in adults than in first-year birds. In summer *adults* of *scolopaceus*, worn rectrices may suggest a first-year bird, but the presence of white terminal margins, especially along the unworn medial side of the rectrix tip, combined with more contrasting barring and more blunt tip outlines, identifies an adult.

In *griseus* these differences do not apply: instead, in most adults, the central pair of rectrices is replaced, rarely others in addition; whereas in first-year birds, most if not all individuals simply retain the rectrices acquired with the first winter plumage.

How these facts affect statistical considerations will be brought out in analyses of mensural characters of the California populations.

PLUMAGE CHARACTERS DISTINGUISHING

L. SCOLOPACEUS AND L. GRISEUS

Skepticism of many avian systematists notwithstanding, a better than 99 per cent separation of long-bills and short-bills in *breeding or juvenal plumages* can be made. The principal plumage characters used in this separation, as well as those of the winter plumages, are now to be reviewed; but it is emphasized that the evidence presented in this paper emerged from simultaneous study of plumage and mensural characters. The reader is asked to assume that the plumage characters described here can be used for separating the two forms and to test the soundness of the separation by examining the evidence from mensural characters which follows. Detailed descriptions of dowitchers are given by Ridgway (1919:196-201); hence the ensuing discussion will be limited to plumage characters serving to distinguish *scolopaceus* from *griseus*.

As pointed out by Conover (1941:377), the long-bill, *L. scolopaceus*, in breeding plumage is characterized by salmon coloration of under parts; white

occurs only as an edging on breast and belly feathers for a brief period after the prenuptial molt, and then not in all specimens. Ventral spotting is dense and confined to the throat and upper breast. The sides of the breast and belly are barred heavily. Dorsally the plumage is dark, the edging and barrings of the black feathers being narrow and reddish buff. The tail feathers are dark, the black bars being relatively wide and the narrow light bars being reddish buff in color (see pls. 1, 4, and 5).

In the short-bill populations of the Pacific coast, variation in ventral color of the breeding plumage is striking (see pls. 2-4). To an almost comparable degree this is also true of the interior Canadian population to be considered later; and although characterizations of this population by Rowan (1932:22) and Conover (1941:379) do not agree, actually both are correct so far as they go and apparently neither is based on material revealing the entire range of variation. Among short-bills of the Pacific coast, under parts may be entirely salmon, usually lighter than, but sometimes as dark as, those of *scolopaceus*. This represents one extreme, the ventral spotting in such birds being sparse and scattered over the entire breast and even the belly, or being obsolete or even absent except on the sides of the breast. In the direction of the other extreme, on some individuals there is a varying amount of white on the mid-belly and vent with varying amounts of spotting. At this extreme, under parts are extensively white, the white reaching anteriorly onto the breast, the buff areas are pale, and the spotting may be extensive and often as dense in western specimens as in eastern specimens to be described later.

Thus, color of under parts in short-billed dowitchers varies conspicuously in two characters: first, extent of spotting, which may be dense and present on both breast and belly at the one extreme, or scattered and light, even absent at the other extreme; second, extent of white, which may be the color of the lower breast and all under parts posteriorly at the one extreme, or lacking (replaced by buff) at the other extreme. To permit analysis of variation in ventral color characters, five arbitrary classes of spotting (A-E) and five of ground color (a-e) were defined, as in table 1. Data on ventral coloration of Californian specimens are given in tables 2 (males) and 3 (females).

There is evidence in tables 2 and 3 of association between ground color and spotting. Specimens with entirely buffy under parts are as richly colored as some specimens of *scolopaceus*, and are sparsely spotted or plain; whereas, specimens whose under parts are duller and more extensively white are more heavily spotted. A 2×2 contingency table was prepared for each sex, the figures for the rows being derived from A + B and C + D + E and those for the columns from a + b and c + d + e. Chi-square values were calculated directly, with adjustment for occurrence of a single low cell value in each of the two tables (Simpson and Roe, 1939:298). The chi-square value obtained for males was 8.80; for females, 10.74. The probability *P* is less than .01 in the calculations for both sexes, and the observed association between ground color and spotting is thus confirmed.

In almost all western specimens of the short-bill, the sides of the breast are spotted, not barred as in *scolopaceus*. In specimens having almost entirely

Pitelka: Geographic Variation in Limnodromus

TABLE 1

ARBITRARY CLASSES IN VENTRAL COLORATION OF LIMNODROMUS GRISEUS

Extent of spotting	Relative extent of rust and white (ground color)
A Heavy on breast; usually light on belly (sometimes obsolete or absent); bars on flanks dense	a Rust on upper breast; white extensive on belly, extending well onto breast
B Moderate on breast; scattered or obso- lete on belly; flank barring moderate	b Rust on breast; belly largely white
C Light on breast; obsolete or absent on belly	c White on mid-belly only
D Obsolete on breast and belly	d White on anal area only
E Obsolete on breast; absent on belly; or under parts immaculate	e White lacking; under parts entirely rust

TABLE 2

FREQUENCY DISTRIBUTION OF MALE DOWITCHERS FROM CALIFORNIA
AMONG VENTRAL COLOR CLASSES

Spotting class	Ground-color class					Total
	a	b	c	d	e	
A.....	0	7	8	1	0	16
B.....	0	12	17	1	1	31
C.....	0	3	14	4	1	22
D.....	0	1	8	4	1	14
E.....	0	0	2	2	0	4
Totals.....	0	23	49	12	3	87

TABLE 3

FREQUENCY DISTRIBUTION OF FEMALE DOWITCHERS FROM CALIFORNIA
AMONG VENTRAL COLOR CLASSES

Spotting class	Ground-color class					Total
	a	b	c	d	e	
A.....	3	14	12	3	0	32
B.....	0	13	13	1	0	27
C.....	0	2	16	2	0	20
D.....	0	1	2	1	0	4
E.....	0	0	3	0	0	3
Totals.....	3	30	46	7	0	86

salmon-colored under parts and thus resembling *scolopaceus*, this spotting, together with the sparsity of mid-ventral spotting, is a color character that serves to distinguish short-bills. All remaining variants are easily distinguished by scattered spotting or white ventral coloration or usually by both.

Although a considerable range of variation occurs in ventral color characters of *L. griseus*, such wide variation is not found in dorsal plumage

TABLE 4

A COMPARISON OF JUVENAL PLUMAGES OF LONG-BILLED AND SHORT-BILLED DOWITCHERS

Plumage character	Long-bill (<i>scolopaceus</i>)	Short-bill (<i>griseus</i> , <i>hendersoni</i> , <i>caurinus</i>)
Color of dorsal patterning	Dark (reddish buff)	Light (light buff)
Extent of patterning	Buff areas narrow and linear; limited to feather margins	Buff areas relatively wide, their margins medial to rachis often irregular; occurring on feather margins and also as subterminal and submarginal bars and marks
Edging of longer tertials	Very narrow and sometimes obsolescent; subterminal bars occasional	Conspicuous without exception; subterminal bars characteristic
Sides of face and neck	More gray	More buff
Barring of tail feathers	Wide, almost black	Bars less wide, dull brownish black
Color of upper breast and neck	Light gray, indistinctly marked, washed lightly with dull buff	Prominently buffy, usually speckled

characters. Most individuals which are richly colored beneath are indistinguishable dorsally from *scolopaceus* except that the rectrices differ in average width of black bars relative to white bars, the former being broader in *scolopaceus*. When the central pair of rectrices has been replaced in the prenuptial molt of *L. griseus*, the light bars on these feathers are thus wider and also lighter than in *scolopaceus*. Individuals which are more white and more spotted beneath, however, have dorsal buff markings which are lighter than those of *scolopaceus*, and in these individuals, furthermore, the coloration of spring-acquired rectrices contrasts even more with those of *scolopaceus* than in the darker individuals of the short-bill.

Thus, specimens of *griseus* and *scolopaceus* in breeding plumage can be classified in two virtually distinct arrays. The suspected identity of any problematical ones can be checked by measurements.

In winter plumages, the long-bill and short-bill do not differ enough to permit separation of all specimens by color characters alone. The tail feathers of *scolopaceus* average considerably darker than those of west coast short-

bills, as pointed out above; but there is overlap in this character between the two forms, as noted by Conover (1941:377). The anterior under parts of *scolopaceus* average darker and more extensively gray, as is pointed out by van Rossem (1945:85), and to a corresponding degree there is less speckling on the anterior under parts and reduced barring on the flanks (see pls. 6 and 7). In *scolopaceus*, the pileum tends to be solid gray, whereas in *griseus*, to varying degree, the feathers are dark gray centrally, light marginally.

In other words, color characters of the winter plumages of the two forms, while not identical, overlap so in adults that they permit a separation of only about 60 to 70 per cent of specimens. This percentage, however, is increased to about 95 per cent when measurements are taken. Moreover, these difficulties do not pertain to birds in first-year winter plumage; the latter can be classified accurately by use of characters of rectrices and other feathers of the juvenal plumage retained through the postjuvenal molt.

Characters serving to distinguish the juvenal plumages of the long-billed and short-billed dowitchers are summarized in table 4 (see also pls. 8 and 9). They have already been recognized by Rowan (1932:25) and Conover (1941:378); used in combination with characters of size discussed below, they rarely offer any difficulty to recognition of the two forms.

Striking differences are found to occur between plumages of the downy young. These are summarized in table 5 (see also pl. 10).

It is concluded that in spite of similarities between *scolopaceus* and *griseus* in certain specific plumage characters, when the latter are considered in combination, discontinuity between the two forms can be demonstrated. Overlap in variability of characters of the winter plumages and similarity of the dorsal patterns of the nuptial plumages are more or less comparable to those found in other species pairs or species groups in the charadriiforms. There is no indication that we are dealing with plumage characters displaying typical quantitative, gradient trends between geographically neighboring, freely interbreeding races. Rather, between *griseus* and *scolopaceus* there are plumage differences of both quantitative and qualitative kinds. There are also differences in degrees of variability of certain characters; although ranges of variation in different characters do transgress, they do not do so to a comparable and consistent degree. We shall return to these points later; here let us note that the sum of the evidence from plumage characters supports the stand taken by Rowan (1932:26), who stated that if true intermediates between *griseus* and *scolopaceus* really exist, they have never been described. All those relatively rare specimens in which plumage characters are not decisive can be identified correctly by use of mensural characters.

ANALYSIS OF CALIFORNIAN POPULATIONS

MENSURAL CHARACTERS

We may begin the analysis of mensural data with those derived from Beck's sample of 311 specimens from Merced County. A startling, initial result of that study in the light of the characters reviewed above was the tentative

TABLE 5
COMPARISON OF DOWNY YOUNG OF LONG-BILLED AND SHORT-BILLED DOWITCHERS

Character	Long-billed Dowitcher (<i>L. scolopaceus</i> ; 10 specimens)	Short-billed Dowitcher (<i>L. g. hendersoni</i> ; 12 specimens from Churchill)*
PATTERN AND COLOR		
General color	Ventrally reddish buff; dorsally dark brown and black with scattered gray feather tips, head and back patterns only slightly contrasting	Ventrally plain buff; dorsally warm buff-brown and black, with prominent scattered white feather tips; head and back patterns contrasting
Superciliary stripe posterior to eye	Narrow, silvery gray	Broad, whitish
Postocular stripe	Relatively broad, chiefly brown, noncontrasting	Relatively narrow, black, contrasting
Dark crown area	Not outlined in black consistently; usually with scattered silver gray tips	Outlined in black; dark and without any light feather tips
Light feather tips on dorsum	Outer 1-mm.† band of silvery gray; barbules apparently sparse‡	Outer 2-mm. band of creamy white; barbules apparently dense
Anal area and lower belly	Dark (brown-black); contrast with reddish buff anterior under parts	Anal area only slightly darker than plain buff anterior under parts
COLOR		
Upper breast	Ochraceous Tawny	Clay Brown
Brown of lower back	Cinnamon Brown	Buckthorn Brown
Iris	Brown§	Black¶
Bill	Black	Dull greenish black
Legs	Olive with blackish stripes down sides	Yellowish olive; darker at joints

* Downy young from Alberta are apparently darker than those from Churchill, Manitoba (Conover, 1941: 379). The brown color of the lower back of three Alberta specimens is not Buckthorn Brown, but redder and darker, nearest Ochraceous Tawny. The darkest area of the anterior under parts is not Clay Brown, but again is darker and redder, tending toward Ochraceous Tawny, but nearest Clay Brown. Comparable differences occur in other buff or brown parts of the plumage.

† Approximate and variable, but width of light color band in *hendersoni* is about twice that in *scolopaceus*, apart from differences in color and feather arrangement.

‡ Difference in barbule density is actually due to the fact that barbs of light-tipped feathers are separated in *scolopaceus*, clumped and terminally attached in *hendersoni*; the stellate or dusty effect of the light spotting seen in *scolopaceus* may be produced in *hendersoni* by separating the barbs of the individual down feather.

§ Colors of soft parts in *scolopaceus* as recorded by H. E. Conover.

¶ Colors of soft parts in *hendersoni* as recorded by W. Rowan from specimens from Fawcett, Alberta.

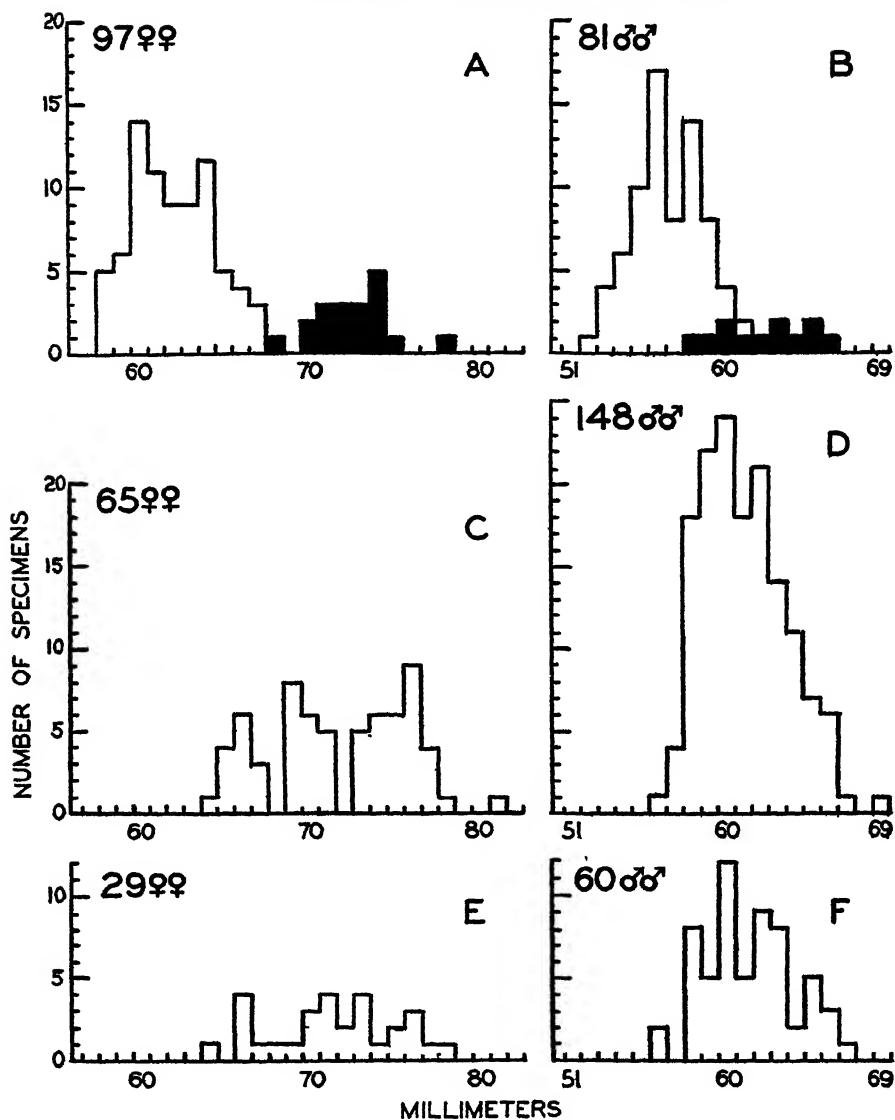


Fig. 1. Variation in length of culmen of adult (C, D) and first-year (E, F) dowitchers from Merced County and of dowitchers (age classes not distinguished) from California studied by Orr, 1941 (A, B); arbitrary separation of long-bills from short-bills, per Orr, *op. cit.*: fig. 18, is indicated in A and B by black squares (long-bills) and light squares (short-bills); all specimens in graphs C-F represent the long-bill (Beck's sample, table 6).

conclusion that all 311 specimens belonged to the long-billed form. Variation in length of culmen of adults (shown in fig. 1, C, D) and first-year birds (E, F) from Merced County was then graphed in agreement with units used by Orr (1940:62; here shown in fig. 1, A, B). Arbitrary separation by Orr of the long-bill (black squares) and short-bill (light squares) is indicated. Dimensions of the series collected by Mr. Beck are given in table 6.

TABLE 6
MEASUREMENTS OF THE LONG-BILLED DOWITCHER (*Limnodromus scolopaceus*) FROM MERCED COUNTY, CALIFORNIA

Dimension	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	Adult.....	64	130-152	145.5 ± 0.4	3.2	2.2
		First-year...	31	137-151	143.9 ± 0.7	3.7	2.5
	♂ ♂	Adult.....	149	130-147	140.2 ± 0.2	2.9	2.1
		First-year...	63	127-146	138.7 ± 0.4	3.4	2.4
Culmen	♀ ♀	Adult.....	65	64.3-80.8	71.72 ± 0.50	4.03	5.61
		First-year...	29	64.5-77.7	71.63 ± 0.67	3.60	5.03
	♂ ♂	Adult.....	148	56.1-68.6	61.21 ± 0.20	2.39	3.90
		First-year...	60	55.7-66.8	61.36 ± 0.33	2.56	4.17
Tarsus	♀ ♀	Adult.....	65	37.7-45.0	41.35 ± 0.20	1.64	3.96
		First-year...	28	37.0-44.5	41.36 ± 0.32	1.68	4.06
	♂ ♂	Adult.....	153	34.8-40.3	37.58 ± 0.10	1.21	3.21
		First-year...	50	35.0-41.1	37.62 ± 0.18	1.40	3.72

TABLE 7
MEASUREMENTS OF THE LONG-BILLED DOWITCHER (*Limnodromus scolopaceus*) FROM CALIFORNIA EXCLUSIVE OF MERCED COUNTY SAMPLE (TABLE 6)

Dimension	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	Adult.....	80	138-156	145.6 ± 0.3	3.1	2.1
		First-year...	70	139-152	144.8 ± 0.4	3.1	2.1
	♂ ♂	Adult.....	68	132-149	140.3 ± 0.4	3.5	2.5
		First-year...	59	132-147	140.0 ± 0.4	3.4	2.4
Culmen	♀ ♀	Adult.....	87	65.5-77.7	71.88 ± 0.27	2.50	3.48
		First-year...	69	65.8-78.5	71.84 ± 0.37	2.86	3.98
	♂ ♂	Adult.....	85	56.6-69.6	61.85 ± 0.32	2.71	4.38
		First-year...	60	54.4-65.7	61.76 ± 0.43	3.35	5.42
Tarsus	♀ ♀	Adult.....	89	38.0-44.6	41.27 ± 0.14	1.31	3.17
		First-year...	69	38.1-44.6	41.13 ± 0.18	1.49	3.62
	♂ ♂	Adult.....	85	34.6-41.2	38.01 ± 0.15	1.42	3.74
		First-year...	61	35.0-40.5	37.81 ± 0.17	1.32	3.49

If color characters indicate all specimens of Beck's sample to be *scolopaceus*, then it is evident that those whose bills fall in length below the arbitrary limits set for *scolopaceus* by Orr (*loc. cit.*) and many earlier authors nevertheless represent the long-billed form. This is substantiated by differences in wing length and tarsal length considered below.

To test my conclusion that all the specimens from Merced County represent *scolopaceus*, and to test further the validity of characters used by Rowan (1932) and Conover (1941) and this writer to distinguish *scolopaceus* from

griseus, I classified all other California-taken specimens according to plumage differences set forth in the preceding section, and calculated statistics for the resulting groups. Data for the long-billed dowitcher are given in table 7, those for the short-billed dowitcher in table 8.

TABLE 8
MEASUREMENTS OF LIMNODROMUS GRISEUS FROM CALIFORNIA

Dimension	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	Adult*	87	143-157	149.9 ±0.3	3.2	2.1
		First-year b †	41	142-156	148.4 ±0.5	3.1	2.1
		First-year a ‡	58	139-155	147.9 ±0.4	3.1	2.1
	♂ ♂	Adult	112	140-153	147.0 ±0.3	2.8	1.9
		First-year b.	28	137-150	144.0 ±0.6	3.2	2.2
		First-year a.	53	135-151	144.8 ±0.5	3.5	2.4
Culmen	♀ ♀	Adult	87	56.8-68.5	61.95±0.25	2.33	3.76
		First-year b.	42	57.5-67.5	61.57±0.34	2.24	3.64
		First-year a.	58	56.6-66.8	60.98±0.33	2.50	4.10
	♂ ♂	Adult	116	52.0-62.1	56.75±0.20	2.12	3.74
		First-year b.	28	53.5-61.0	57.03±0.26	1.38	2.42
		First-year a.	53	52.3-60.9	57.57±0.27	1.96	3.40
Tarsus	♀ ♀	Adult	87	34.8-41.0	37.54±0.14	1.31	3.49
		First-year b.	43	34.7-40.7	37.60±0.22	1.47	3.91
		First-year a.	57	34.8-41.2	37.94±0.19	1.44	3.79
	♂ ♂	Adult	113	33.6-39.7	36.50±0.11	1.22	3.34
		First-year b.	29	33.9-39.1	36.59±0.23	1.24	3.39
		First-year a.	53	33.5-39.2	36.95±0.17	1.28	3.50

* Some first-year birds included (see text).

† Specimens collected in March-August, classed as first-year birds but representing less than 100 per cent of that age group (see text).

‡ Specimens in juvenal plumage or postjuvenal molt, thus representing a distinct age group; six collected in November and December, all others in August-October.

Comparison of tables 6 and 7 reveals a close agreement in dimensions of these two groups. No statistically significant differences occur between corresponding sex and age groups. These results support the conclusion that all 311 specimens in Beck's series from Merced County represent *scolopaceus*. The tables also demonstrate that in *scolopaceus* no significant differences occur between first-year and adult birds in length of culmen and tarsus. Data for these two dimensions from the two age groups will henceforth be combined.

Comparison of either table 6 or 7 with table 8 reveals differences not only of significant degree, but also of opposing trend. Thus, whereas the tarsus of the short-billed form is shorter than that of the long-billed form, the wing is longer. All these data indicate that, in spite of the overlap in ranges of corresponding dimensions, the observed variabilities are normal or almost so and comparable in the two forms.

Furthermore, table 8 demonstrates that in *griseus* also no significant differences occur between first-year and adult groups in length of culmen and tarsus. With regard to wing length, fall- and winter-taken first-year birds can be segregated without difficulty; but, for reasons given in the foregoing section on molt, a complete separation of first-year and adult specimens in spring plumage cannot be made. However, at least a partial separation must be made if as accurate as possible a figure on wing length of adults is to be obtained. In an occasional specimen, one or several juvenal rectrices are retained through the winter; more frequently, one or several juvenal scapulars are retained; and in most first-year birds, wear of the remex tips is marked by spring, whereas in adults, with a great part if not most of their migratory flight still ahead of them, the remex tips are unworn or only slightly worn. By thus segregating spring-taken specimens into adult and first-year groups, figures for wing length shown in table 8 are obtained. Apparently the separation was reasonably successful in females, in which the mean wing length for spring-taken first-year birds ("b" group) is closer to that of the fall-taken, undoubted first-year birds ("a" group) than to that of the adults. However, some first-year birds are almost certainly included in the adult category, and it may be concluded that the calculated mean wing length of adults, 149.9 mm., is slightly smaller than the true value. The separation seems to have been more successful in males, in which not only is the difference between adults and the "a" group greater, but the value for wing length of the "b" group falls below that of the "a" group, as is to be expected since the same feathers, worn by spring, are measured.

It is concluded that the criteria for distinguishing long-billed and short-billed forms as set forth by Rowan (1932) and Conover (1941) are valid. If any other combination of color characters were used to separate *scolopaceus* from *griseus*, the statistical differences demonstrated above would be obscured through greater variability and greater overlap thereof. This state of affairs must have resulted in Brodkorb's (1933:125) work, as is evident in the following quotation: "Contrary to [Rowan's] statement, . . . intermediates between [long-billed and short-billed forms] are by no means rare. Over twenty individuals of the series examined [total, 186] in the present connection are not typical of either race." I can only say that according to criteria used in this work no such equivocal intermediates were seen. Brodkorb (*op. cit.*:124) correctly pointed out that the wing of *scolopaceus* averages shorter, the culmen and tarsus longer, than in *griseus*; but his measurements of these two forms differ less than those given in tables 7 and 8, and this again indicates unsuccessful segregation of specimens, especially when we realize that his material of "*griseus*" included a good many specimens of *L. g. hendersoni*, an interior race smaller than *caurinus* of table 8. Also, he did not distinguish age classes, and for this additional reason his data are not conclusive.

Much the same difficulties are encountered if an arbitrary figure of bill length is used as a criterion to separate the two forms. Thus, Orr (1940:61) and others have classified any female with a bill length of 68 mm. or more as the long-bill and any of 67 mm. or less as the short-bill. Had color char-

acters been evaluated correctly, it would have been apparent that this criterion was invalid, inasmuch as specimens whose color characters unmistakably place them in the long-billed group fall below arbitrary limits set by Orr for both male and female groups and are then called *griseus*! (See fig. 1 and compare with tables 6 and 7.)

The distinctness and biological integrity of either population is further demonstrated by the fact that, if mensural characters of corresponding sexes are compared, they are found to differ in magnitude between sexes. If average

TABLE 9
SUMMARY OF WEIGHT RECORDS*

Species and sex	Number of records	Range	Mean	Per-cent difference in males (females, 100 per cent)
<i>L. g. caurinus</i>				
Females.....	8	101-123	110.8 gr.	
Males.....	10	91-133	106.3	-4.1
<i>L. g. hendersoni</i>				
Females.....	11	95-140	114.8	
Males.....	9	91-145	108.4	-5.6
<i>L. scolopaceus</i>				
Females.....	11	93-131	114.7	
Males.....	7	90-114	99.9	-12.9

* Obtained, with one or two exceptions, from individuals collected in migration, in both spring and fall, in the United States and British Columbia.

dimensions of *griseus* (table 8), considered as 100 per cent, are compared with those of *scolopaceus* (table 7), the differences between adults are as follows:

Females: wing, -2.9 per cent; culmen, +16.0; tarsus, +9.9.

Males: wing, -4.6 per cent; culmen, +9.0; tarsus, +4.1.

Thus, in bill length, for example, females of *scolopaceus* are 16.0 per cent larger than females of *griseus*, whereas in males this difference amounts to only 9.0 per cent. These data clearly indicate that, in mensural characters, degree of sexual dimorphism differs in the two forms. Differences between females (100 per cent) and males in the two forms are as follows:

L. scolopaceus: wing, -3.6 per cent; culmen, -14.0; tarsus, -7.9.

L. griseus: wing, -1.9 per cent; culmen, -8.4; tarsus, -2.8.

Available weight data are summarized in table 9. If per cent differences between sexes for the two populations of *L. griseus* represented there are averaged, a value of 4.9 is obtained. The differences (per cent) between sexes in weight of *scolopaceus* and *griseus* may be compared with those of tarsal length. The ratio for weight, 4.9:12.9, is approximately the same as that for tarsus, 2.8:7.9. Thus, *scolopaceus* differs from *griseus* in magnitude of sexual

difference not only in several linear dimensions, but also in weight, the difference in which is proportional to that of tarsal length.

The fact of dissimilar contrasts between sexes of the two forms in comparative size of bill has been pointed out by Rowan (1932:21) and Conover (1941:376). Rowan (*op. cit.*:22) was also aware, in a general way, of the other discrepancies in sexual dimorphism, but, because only a small number of specimens was measured and because adults were not distinguished from first-year birds, these differences were not measured precisely.

ECOLOGICAL DISTRIBUTION

We may again return to Beck's sample of 311 specimens from the San Joaquin Valley. It was concluded in an earlier section that all these represented *L. scolopaceus*; and, as was demonstrated in figure 1, these results differ from

TABLE 10
SUMMARY OF 541 SPECIMEN-RECORDS FROM MERCED COUNTY, CALIFORNIA

Period	Beck's sample (<i>L. scolopaceus</i>)		All other specimens			
			<i>L. scolopaceus</i>		<i>L. griseus</i>	
	Males	Females	Males	Females	Males	Females
March-May.....	146	70	68	74	11	8
June-July.....	4	4	1	1	..	1
August-October....	35	11	27	24	.	..
November-February.	31	10	7	8
Totals.....	216	95	103	107	11	9
Grand Totals.....	311		210		20	

those of Orr (1940:63), who, after a study of specimens available in the California Academy of Sciences, decided that the short-bill was about five times more common in California than the long-bill. My results do not necessarily invalidate Orr's data, but they do show that his conclusions were incorrect and that some fundamental feature of local distribution of Californian dowitchers remains unclarified.

It is first of all desirable to take Merced County as a sample area and examine all specimen records along with those of Beck. The data are summarized in table 10. Only 20 out of a total of 541 specimen-records, or 3.7 per cent, represent *L. griseus*. Orr's 5 to 1 ratio was based on 178 specimens; here, on the basis of 541 specimens, we have a reversed ratio of 1 to 26!

This difference can be resolved if an ecologic segregation between the two forms occurs, the long-bill mainly in fresh-water habitats, the short-bill in tidal, brackish, or salt-water habitats. By this suggestion I do not imply that a differential tolerance to salinity *per se* occurs in dowitchers, but rather that there are differences in preference for kind of feeding substrate and in feeding behavior.

All the Merced County specimens were obtained in fresh-water habitat. Of the 207 specimens available to Orr in the California Academy of Sciences in 1940, 178 from California were used as basis for conclusions concerning occurrence in that state. In 1946, I examined a total of 206 Californian specimens in the same collection, including those studied by Orr. Of these, 169 were short-billed dowitchers, and 162 of them were collected at salt- or brackish-water localities, chiefly in the San Francisco Bay region. The remaining 37 were specimens of the long-billed dowitcher, and only 9 of these were collected at salt-water localities. Thus, on the basis of the Merced County sample and Orr's data, an ecologic segregation of the two forms is demonstrated, and Orr's erroneous conclusion is explained by the small representation in the Academy's collection of specimens taken at fresh-water localities. What Orr's data do suggest, of course, is that in California the short-billed dowitcher is common at salt- or brackish-water localities, whereas the long-billed dowitcher apparently prefers fresh-water habitats.

Since the fact of ecologic segregation first became apparent in the early phases of my study, I have learned that Beck (letter) has been aware of it. Van Rossem (1945:85) also refers to it, but otherwise this differential local distribution in dowitchers has been overlooked by observers on the Pacific coast.

To test this habitat segregation in a conclusive manner and to attempt a percentage measure of relative occurrence in different habitats, all complete specimen-based records from California were classified to show whether habitats present at each were fresh water or salt water. Brackish-water areas are classified as "salt-water localities" (symbol S in tables 11 and 12), the important habitat feature being the periodically exposed tidal flats. Fresh-water localities were subdivided geographically into those near the coast (FC) and those east of the Coast Ranges (FI), chiefly in the Sacramento and San Joaquin valleys. Localities identified in accordance with this scheme are listed in the Appendix, below. Some doubt may arise in classification of localities near or bordering brackish- or salt-water habitat where also some fresh-water habitat may occur, as, for example, Redwood City on San Francisco Bay. But any fresh-water marshes or ponds, if indeed they afford habitat suitable for dowitchers, are negligible areally in proportion to the extent of the marine littoral; and over most of coastal California, physiography is so varied that fresh-water marshes and ponds are comparatively rare. For these reasons all localities bordering the coast, bays, or any inlets having tidal flow were arbitrarily classified as salt-water localities. In my opinion, the error introduced by this procedure into the figures now to be given is slight and negligible.

If specimens are tabulated by type of habitat where taken, and with respect also to sex, age, and time of year, the data shown in tables 11 and 12 are obtained. In the long-billed dowitcher (table 11), 90.9 per cent of a total of 638 specimens were obtained at fresh-water sites; in the short-billed form (table 12), 93.2 per cent of a total of 398 specimens were obtained at salt- or brackish-water sites. Thus, a remarkable degree of ecological segregation is shown to occur.

TABLE 11
HABITAT PREFERENCE OF LIMNODROMUS SCOLOPACEUS SHOWN BY 638 CALIFORNIA SPECIMENS

Date	Males						Females					
	Adult			First-year			Adult			First-year		
	S*	FC*	FI*	S	FC	FI	S	FC	FI	S	FC	FI
Jan.....	8	1	..	5	5	2	2	1
Feb.....	10	2	..	2	2	..	3	3
Mar. 1-7.....	8	3	15	3
8-15.....	8	1	1	4	4	2	1	2
16-23.....	10	5	9	4
24-31.....	16	1	1	..	2	4
April 1-7.....	3	..	12	1	..	5	1	..	4	1	..	4
8-15.....	22	1	1	13	18	..	1	6
16-23.....	3	..	23	4	..	8	16	1	..	10
24-31.....	23	2	..	10	2	..	11	1	..	9
May 1-7.....	..	2	18	4	4	11	2	2	20	3	3	7
8-15.....	1	..	3	8	4	4
16-23.....	1
24-31.....	1
June.....	1
July 1-7.....	1	1
8-15.....	3
16-23.....
24-31.....	3	2	1
Aug. 1-7.....	5	5	6	3
8-15.....	4	3	3	2
16-23.....
24-31.....	7	1†	3	1†
Sept. 1-7.....	1	..	2	2
8-15.....	4
16-23.....	1	2†	3	1†
24-31.....	13	1	..	4	5	5
unspecified..	1
Oct. 1-7.....	4	2	1	4
8-15.....	4	1	2
16-23.....	4	3	1	..	1	1
24-30.....	4	2	4	1	..	1
Nov.....	4	2	1	2	..	5
Dec.....	5	1	..	3	2	..	2	1	..	1
Totals.....	8	2	231	24	6	102	10	2	142	16	8	87
Percentages.....	1.3	0.3	36.2	3.8	0.9	16.0	1.6	0.3	22.3	2.5	1.3	13.6

* S, salt or brackish-water habitat; FC, coastal, fresh-water habitat; FI, interior fresh-water habitat.

† All July and August records in this age group represent birds one year old passing into the first complete molt, or about to do so, after which they are indistinguishable from adults.

‡ All September records in this age class represent birds in juvenal plumage or undergoing postjuvenal molt.

TABLE 12
HABITAT PREFERENCE OF LIMNODROMUS GRISEUS SHOWN BY 398 CALIFORNIA SPECIMENS

Date	Males				Females			
	Adults		First-year		Adults		First-year	
	S	FI	S	FI	S	FI	S	FI
Jan.....	3	3
Feb.....	1
Mar. 1-7.....	..	1	Age classes combined		Age classes combined	
8-15.....	12	..			1	..		
16-23.....	13	..			6	..		
24-31.....	4	..			4	..		
April 1-7.....	27	..			11	..		
8-15.....	10	1			12	..		
16-23.....	11	6			16	5		
24-30.....	15	2			10	2		
May 1-7.....	4	4			7	3		
8-15.....	2*	..			5	1		
16-23.....	6*	..			7†	..		
24-31.....	1*	..			3‡	..		
June.....	2§		
July 1-7.....	..	1§			2§	..		
8-15.....	6§	..	2¶	..	27§
16-23.....	6§	5§	..	2¶	..
24-31.....	2§	2§
Aug. 1-7.....	2§
8-15.....	2	3	..
16-23.....	1	..	17	15	..
24-31.....	1	..	19	..	1	..	10	..
Sept. 1-7.....	7	13	1
8-15.....	3	3	..
16-23.....	1	1	..
24-30.....	1	2	..
Oct. 1-7.....	1	..
8-15.....	2	..
16-23.....	1	..	1	..	3	..
24-31.....	2
Nov.....	1	..	3	..
Dec.....	2	..	2	..	1	..
Totals.....	128	15	57	0	127	11	59	1
Percentages.....	32.2	3.8	14.3	0	31.9	2.8	14.8	0.3

* Including one specimen in winter plumage, apparently first-year individual and nonbreeder.

† Including three such specimens.

‡ Including two such specimens.

§ Nonbreeding individuals; most if not all are first-year birds, many of them with mixed plumage.

¶ Young of the year, in juvenal plumage.

SEASONAL OCCURRENCE

By inspection of table 11, it is further evident that most of the records of the long-bill at salt-water localities fall into the seasons of migration, periods when ecological displacements in general are most frequent among birds which migrate. Thus, salt-water records (table 11) in March, April, and May, and in August, September, and October, make up 43, or 74 per cent, of the year-round total of 58.

It is desirable to examine the data with respect to relative occurrence of adult versus first-year long-billed birds at salt-water localities. A summary of the available figures follows:

March-May (34 records): adult birds, 38 per cent; first-year birds, 62 per cent.

June-July (2 records): adult birds, none; first-year birds, 100 per cent.

August-October (9 records): adult birds, 11 per cent; first-year birds, 89 per cent.

November-February. (13 records): adult birds, 31 per cent; first-year birds, 69 per cent.

Total of 58 records: adult birds, 31 per cent; first-year birds, 69 per cent.

Thus, more first-year birds than adults occur at salt-water localities. Whether they do so relatively less in the spring, as is suggested by the data just given, cannot be stated since the samples from other periods of the year are too small.

In the salt-water form, the short-billed dowitcher (table 12), the majority of individuals recorded in fresh-water habitat also fall into the migration seasons, thus complementing the situation in the long-billed form. Of a year-round total of 27 fresh-water records, 24, or 89 per cent, fall in April and May. Only one fresh-water record is available for autumn. No records of the short-billed dowitcher were obtained at fresh-water coastal localities, and this category is accordingly absent from table 12.

Records of the short-billed dowitcher cannot be analyzed to the same degree as those of the long-billed form, because it is not possible satisfactorily to separate first-year and adult birds after midwinter (see p. 6). However, certain interesting comparisons between *griseus* and *scolopaceus* may be made. First, there is an astonishing absence of adults of the short-bill in the fall (see table 12), whereas among long-bills, the sample of which is smaller, representation of adults is greater. This difference suggests that adults of the short-bill may migrate southward without extended stopover along the Californian coast, whereas the young are not so definite in their behavior and migrate over a longer period; not that they are necessarily slower than the adults, but they spend more time in wandering and at stopover localities.

The probability that in California the fall period of migratory occurrence of adult short-bills is indeed shorter than that of young short-bills, or of the long-billed form, is strengthened by two facts: (1) winter records of the short-bill are less numerous than those of the long-bill, and (2) the winter range of the short-bill extends farther south. With reference to the first point, of a total of 91 California records of dowitchers in the months November through February (tables 11 and 12 combined), 75, or 82 per cent, represent the long-billed form. This is interpreted as indicating that a greater proportion of the short-bill population passing through California winters farther south

than is true of the long-billed population. The winter range of the short-bill extends south to Peru and Brazil, that of the long-bill only to Guatemala.

Further comparison of tables 11 and 12 might indicate that nonbreeding individuals of the short-billed form occur in the summer much more commonly than those of the long-billed form. Specimens collected in June and July total 53 nonbreeding short-bills, 12 nonbreeding long-bills. But the

TABLE 13
OCCURRENCE OF DOWITCHERS IN CALIFORNIA IN MIGRATION PERIODS

Species		March		April		May		Total	
		1-15	16-31	1-15	16-30	1-15	16-31		
Long-billed dowitcher									
Number of specimens*.....		52	52	93	128	96	2	423	
Per cent.....		12.3	12.3	22.0	30.3	22.7	0.5	100.1	
Short-billed dowitcher									
Number of specimens*.....		14	27	61	67	26	17	212	
Per cent.....		6.6	12.7	28.8	31.6	12.3	8.0	100	
	July 23-31	August		September		October			
		1-15	16-31	1-15	16-30	1-15	16-31		
Long-billed dowitcher									
Number of specimens									
Adults.....		3†	18†	10	9	22	9	13	84
Juveniles.....		0	0	0	0‡	13	9	9	31
Short-billed dowitcher									
Number of specimens									
Adults.....		0	0	3	0	0	0	1	4
Juveniles.....		4	5	61	27	5	3	6	111

* Adult and first-year birds combined.

† It is doubtful that these all represent migrants arrived from breeding grounds.

‡ Juveniles appear in this period even though records are lacking here; viz., a male (MCZ 217688) collected in Baja California on Sept. 2 (1887). See also table 14.

sample is biased and inadequate since 35 of the 53 short-bills were collected on San Francisco Bay at Alameda between July 9 and 20, 1909 (specimens in the California Academy of Sciences).

A valid comparison is to be made, however, with respect to periods of migration, data for which are summarized in table 13. No difference is apparent in the spring; in the fall, however, a significant difference appears. Considering only the young-of-the-year, specimens of the short-bill were collected from July 23 through October, but 79 per cent of them were obtained between August 16 and September 15; whereas no specimen of the long-bill was obtained until September 18, and 71 per cent of the specimens were collected between that date and October 15. Data on periods of migration from southern British Columbia, Washington, and Oregon (table 14) are adequate for the

long-bill but not for the short-bill; nevertheless, they are in agreement with those from California and support the conclusions based on the California data.

In an analysis of the migration of *L. g. hendersoni* and *L. scolopaceus* through eastern Nebraska, Swenk (1940:71-72) reached conclusions almost parallel to those given above: No difference occurred in the time of spring migration. Fall records of short-bills were scarce, and but two were reported, August 29 and September 15. Remaining fall records represented long-bills, occurring "mostly in the month of October" and "averaging about October 17." Dowitcher records from western Nebraska were considered to represent only long-bills.

TABLE 14
SUMMARY OF 72 RECORDS OF JUVENAL SPECIMENS FROM SOUTHERN
BRITISH COLUMBIA, WASHINGTON, AND OREGON

Date	<i>L. scolopaceus</i>	<i>L. griseus</i>
August 1-15.....	0	6
August 16-31.....	0	10
September 1-15.....	8	2
September 16-30.....	22	2
October 1-15.....	17	0
October 16-31.....	0	0
November 1-30.....	5	0
Totals.....	52	20

In summary, it has been shown that dowitchers of a given species occur in an atypical habitat chiefly in periods of migration, and that, of *scolopaceus* at least, first-year birds make up the majority of them. Adult short-bills apparently move southward in the fall without extended stopover. Juveniles of the short-bill migrate earlier than those of the long-bill. This probably holds true of adults also.

ANALYSIS OF OTHER POPULATIONS OF LIMNODROMUS SCOLOPACEUS

DISTRIBUTION

The long-billed dowitcher breeds along the western and northern coasts of Alaska, from Hooper Bay and the Kashunik River north to Point Barrow and Point Tangent, and, according to MacFarlane (1891:426), eastward along the Arctic coast to the Anderson River. It is apparently to MacFarlane's record that Bent (1927:121) and more recent authors refer when they cite Franklin Bay as the eastern outpost of breeding occurrence. But according to J. L. Peters (letter), the Museum of Comparative Zoology, Harvard University, contains a set of eggs collected on Franklin Bay, June 11, 1901, by H. H. Bodfish. Among specimens examined in this study, I have seen only seven collected east of Point Tangent: a first-year specimen (CM 157967,

labeled female, but male according to dimensions: bill length 60.2 mm., wing 139, and tarsus 37.1), together with four downy young collected on July 20, 1933, at Collinson Point, 250 miles east of Barrow; and two juveniles, collected on August 20, 1914, on Herschel Island, on the Yukon coast near the Alaskan boundary. There is also a breeding record from the mouth of the Kuparuk River, Alaska (Anderson, 1913:472); but records from northern

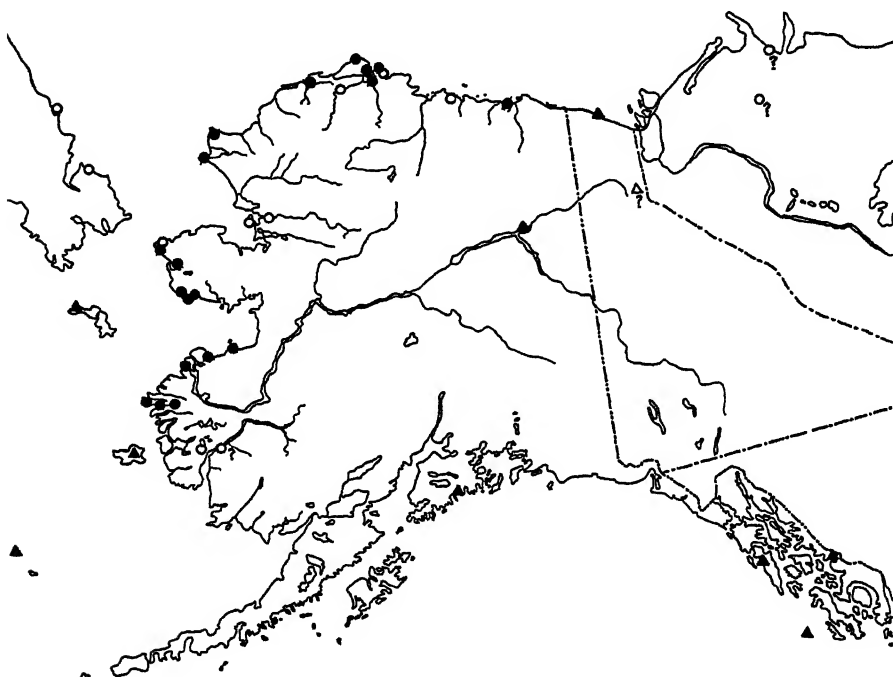


Fig. 2. Distribution of *Limnodromus scolopaceus* in Alaska. Solid dots indicate records of summer occurrence; solid triangles indicate records of migrants; hollow symbols (circles and triangles) indicate records from literature. Queried records in northwestern Mackenzie and northern Yukon (those in the former province representing actual breeding records) are only tentatively assigned to *L. scolopaceus*.

Yukon and northwestern Mackenzie are only tentatively assigned to *scolopaceus* since no breeding specimens have been examined from these areas. South of Hooper Bay, the long-billed dowitcher was observed near the Kuskokwim River in June, 1878, by Turner (1886:146), and in the period June 4-12, 1946, Walkinshaw and Stophlet (1949:31) observed dowitchers on four different days thirty miles west of Bethel. These records suggest that *L. scolopaceus* may breed farther south than it is now known to do. A set of eggs of a dowitcher was collected at Goodnews Bay, southeast of Kuskokwim Bay, by D. Bernard Bull on June 6, 1932, but whether these eggs represent *L. scolopaceus* or *L. griseus* cannot be settled without specimens of breeding birds. (See fig. 2.)

L. scolopaceus has been found west of Bering Strait, but apparently only as a vagrant. Pleske (1928:240) reports three records from the Chukchi Peninsula in northeastern Siberia, and I have examined a first-year male taken there in June, 1869 (MCZ 154058). There are two records from the Northwest Pacific area, a first-year female collected at Achi-Shibito, East Yezo Island [Hokkaido], Japan, on October 13, 1874 (US 95950), and a specimen in winter plumage, not seen by me and tentatively assigned to *scolopaceus*, collected at Yokohama, Japan, on March 13 (year ?) (Seeböhm, 1884:33; Bent, 1927:122).

In migration, *scolopaceus* occurs chiefly along the Pacific coast, in interior Canada (Alberta, Saskatchewan, Manitoba), and in the larger basins and

TABLE 15

MONTHLY DISTRIBUTION OF EAST-COAST RECORDS OF PILE LONG-BILLED DOWITCHER

(See list of 61 specimens by localities, page 70; one unsexed adult omitted below)

Sex	Age	Month														Total
		A	S	O	N	D	J	I	M	A	M	J	J	A	No date	
♀ ♀	Adult	0	0	1	0	0	0	3	2	1	1	0	0	0	1	12
	First-year	0	4	1	0	1	0	0	2	3	0	0	2	3*	2	18
♂ ♂	Adult	0	1†	0	1	1	0	4	0	1	0	0	0	0	1	9
	First-year	2‡	2	3	0	2	0	2	1	4	0	0	2	3*	0	21
																60

* Specimens slightly more than one year old, approaching or undergoing first complete molt

† Specimen passing through first complete molt (MCZ 139922), all other September specimens are juveniles

‡ Juveniles. Unsexed individual (probably ♂, judging by dimensions), "August, 1880," Rockaway, Long Island (AM 45612), male, August 29, 1895, Nantucket I., Mass. (US 161349)

valleys of the United States eastward to the Mississippi Valley, and southward into Baja California, Mexico, and along the Gulf coast. Three specimens collected in eastern Canada have been examined: two from Ontario, and a juvenal male (AM 357158) from Sable Island, Nova Scotia, taken on October 31, 1897, a record which represents the northernmost occurrence of *scolopaceus* on the Atlantic coast.

Along the Atlantic coast, the long-billed dowitcher is relatively uncommon. The available specimen records are summarized in table 15. If there are added the specimens used in this study which were taken in the provinces and states from Nova Scotia southward to and including Florida are added, those of *scolopaceus* total 61, those of *griseus*, 505. Assuming random collection of these easily confused forms, only about 10 per cent of the dowitchers occurring along the eastern coast represent *scolopaceus*. The percentage would be even smaller if it were admitted that collectors may select long-billed birds in the hope of collecting *scolopaceus* and if, as was done with *scolopaceus*, all Floridan specimens of *griseus* were included in this calculation instead of only those from the Atlantic side of the peninsula.

According to several reports in the literature (see, for example, Urner and Storer, 1949), *scolopaceus* and *griseus* are supposed to differ in period of fall migration on the Atlantic coast. In the light of data from California, this is not unlikely, but the specimen evidence on the Atlantic coast is scanty. The earliest fall record of a juvenile of *scolopaceus* is a male collected on Nantucket Island, Massachusetts, August 29, 1895. The earliest fall record of an unquestioned adult cannot be given, since a September or October specimen in adult plumage may be a bird which has passed through only the first complete molt and may have spent the summer south and east of the breeding range. Thus, the four July records shown in table 15 represent vagrant non-breeders (see table 16, p 28). This appears to be true also of the six August records. The one September record is that of a specimen apparently passing through the first complete molt.

The main southward movement of *Limnodromus griseus* on the Atlantic coast occurs in July and August (Stone, 1937:480). Thus, the best that can be said from the records summarized in table 15 is that twelve birds-of-the-year of *scolopaceus*, unquestionably arrived from breeding grounds, were collected in late August, September, and October, *after* the main period of fall migration of *L. griseus*.

The winter range of *L. scolopaceus* extends from interior central California (Pierce, Solano County; 4 mi. NE Oakley, Contra Costa County; Stockton, San Joaquin County), San Francisco Bay (Novato, San Francisco, Alameda, and five localities around the southern arm of the bay), the southern Californian coast (Wilmington and San Pedro, Los Angeles County), Chihuahua (Colonia Díaz), Texas (Rockport, Santa Maria, Brownsville), Louisiana (Cameron; Vermillion Parish), and Florida (Kissimmee Lake, Upper St. John River, Florida Keys), southward through Baja California and Mexico to Chiapas (Belén, Las Garzas) and Guatemala (localities unspecified). Only specimens collected in the four-month period from November to February and examined by me have been used in preparing this statement of winter range. Winter-taken specimens, apparently vagrant individuals, collected north of this range are as follows: adult male, Erie Township, Monroe County, Michigan, December 5, 1943; adult male, Turtle Island, South Carolina, November 30, 1929; first-year specimen (sex?), Sauvies Island, Multnomah County, Oregon, November 3, 1937; and first-year female, Lulu Island, British Columbia, November 23, 1935.

No specimens of *scolopaceus* have been examined from any localities south of Guatemala (see table 26, p. 46); those reported in the literature which I have been able to examine have all proved to belong to *L. griseus*. Readers interested in the disposal of these records may refer to the synonymies of *L. griseus*, pages 72-76 of the Appendix.

Nonbreeding individuals occur scatteredly in regions where the long-billed dowitcher is regularly present as a migrant, winter resident, or both, and also in regions where the species is only a casual visitant. All such records for the period from June 1 to July 15 are summarized in table 16. Late July or early August records were included if condition of plumage, age category,

distance from breeding grounds, or other circumstances, singly or in combination, indicated that the specimens in question were nonbreeding individuals. Because of this strict selection, some late July or early August records of bona fide nonbreeders have probably been omitted. Conversely, it is possible that a few early July specimens (for example, the three adult females from Alberta) may be migrants.

TABLE 16
OCCURRENCES OF NONBREEDING INDIVIDUALS OF *LMNODROMUS SCOLOPACEUS*
(All first-year birds, unless indicated otherwise)

State or province	Date	Plumage		
		Summer	Mixed	Winter
Texas	June 9-July 18	1 ♀	2 ♂	
New Jersey	August 7	1 ♀		
New York	July 23-24	2 ♂, 1 ♀		
	August 7-14	2 ♂		
	August ?	1 ♀		
	August 19	1 ♂		
Massachusetts	July 23	1 ♀		
New Hampshire	August 2		1 ♀	
	July 22-25		3 ♂	
Michigan	August 5		1 ♂, 2 ♀	
	August 10-12		1 ♂, * 3 ♀ *	
	July 10-15	2 ♂, 4 ♀ †		
North Dakota	July 13	1 ♀		
Utah	July 16-28	3 ? ♂, 10 ♀		
Nevada	August 11	3 ♂, 1 ♀		
California	June 3-July 10	1 ♂, 6 ♀		
Oregon	June 12	1 ad. ♂		
Washington	June 10			1 ad. ♀ ‡
Totals		42	13	1

* Undergoing first complete molt, earlier than normal; this is also true of four specimens collected at Dundurn, Sask., on August 18, 1939.

† Three of these females are adults.

‡ A puzzling specimen in fresh winter plumage of an adult female, collected June 10, 1911, at North Yakima, Wash. (LCS 7927). The label bears the notation, "Fall plumage killed in the spring."

Table 16 establishes three facts: first, nonbreeding individuals of *L. scolopaceus* may spend the summer in scattered parts of either the winter or migratory range; second, most of them (89 per cent, in table 16) are first-year birds approaching the first complete molt; and third, most of the individuals listed in table 16 (75 per cent) underwent a first prenuptial molt. The last point may apply only to nonbreeding individuals along migratory routes, since these preponderate in table 16, and thus not necessarily to specimens from areas of winter residence.

VARIATION

Data on mensural characters of *L. scolopaceus* from areas other than California are given in tables 17-19. The areas represented are, respectively, Alaska (chiefly summer-taken breeding specimens); interior Canada, where,

TABLE 17
MEASUREMENTS OF THE LONG-BILLED DOWITCHER (*LIMNODROMUS SCOLOPACEUS*)
FROM ALASKA

Dimension	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	Adult.....	17	138-151	143.7 ±0.7	2.9	2.0
		First-year...	17	139-149	142.5 ±0.7	2.8	2.0
		Juvenal.....	30	141-152	147.2 ±0.5	2.7	1.9
	♂ ♂	Adult.....	20	133-143	138.9 ±0.7	3.1	2.2
		First-year...	27	133-144	138.6 ±0.5	2.6	1.9
		Juvenal.....	47	136-147	142.1 ±0.4	2.9	2.0
Culmen	♀ ♀	Adult and first-year	34	64.2-76.2	71.64±0.37	2.10	2.93
		Juvenal.....	30	65.4-75.5	70.65±0.50	2.73	3.86
	♂ ♂	Adult and first-year..	47	56.8-68.6	62.14±0.40	2.73	4.39
		Juvenal.....	47	56.3-67.3	60.53±0.38	2.61	4.31
Tarsus	♀ ♀	Adult and first-year..	33	38.7-44.9	41.05±0.28	1.63	3.97
		Juvenal.....	30	38.1-44.4	41.35±0.31	1.72	4.16
	♂ ♂	Adult and first-year..	47	34.7-41.2	38.19±0.22	1.48	3.88
		Juvenal.....	47	34.9-42.3	37.98±0.28	1.90	5.00

TABLE 18
MEASUREMENTS OF THE LONG-BILLED DOWITCHER (*LIMNODROMUS SCOLOPACEUS*)
FROM ALBERTA, SASKATCHEWAN, AND MANITOBA

Dimension	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	Adult.....	19	148-150	143.2 ±0.6	2.6	1.8
		First-year...	16	148-150	143.2 ±0.7	2.9	2.0
		Juvenal.....	19	139-151	145.9 ±0.7	2.9	2.0
	♂ ♂	Adult.....	17	133-144	138.6 ±0.7	2.9	2.1
		First-year...	15	134-145	138.6
		Juvenal.....	18	134-146	139.9 ±0.9	3.9	2.8
Culmen	♀ ♀	58	65.3-78.4	72.29±0.38	2.87	3.97
	♂ ♂	59	55.3-69.3	62.45±0.32	2.49	3.99
Tarsus	♀ ♀	59	37.7-45.3	41.55±0.22	1.66	4.00
	♂ ♂	60	35.7-41.5	38.58±0.24	1.89	4.90

as migrant and nonbreeding summer visitant, *scolopaceus* occurs with *griseus*; and the Atlantic coast. In these tables, data for length of culmen and tarsus from first-year and adult specimens are combined because no significant differences appear between the two age groups in tables 6 and 7. Comparisons of the five tables, 6, 7, and 17 through 19, reveal no irregularities in the statistics for culmen and tarsus. This further substantiates the basis for separating *scolopaceus* from *griseus* by plumage characters described earlier.

The same is true of the statistics for wing length, some seeming irregularities notwithstanding. For this dimension, age groups have been kept separate.

TABLE 19
MEASUREMENTS OF THE LONG-BILLED DOWITCHER (*Limnodromus scolopaceus*)
FROM THE ATLANTIC COAST

Dimension	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	Adult.....	12	139-149	144.4
		First-year...	15	137-150	143.7
	♂ ♂	Adult.....	8	133-142	138.4
		First-year...	19	134-146	140.0 ±0.7	3.0	2.1
Culmen*	♀ ♀	28	68.4-76.9	72.16±0.45	2.37	3.28
	♂ ♂	28	56.9-67.2	62.91±0.47	2.50	3.97
Tarsus*	♀ ♀	28	37.6-44.2	41.29±0.28	1.49	3.61
	♂ ♂	27	36.2-41.4	38.32±0.24	1.23	3.21

* Adult and first-year birds combined for these dimensions.

The irregularities just mentioned are the rather surprising differences between wing lengths of Alaskan juveniles and those of adults of both sexes, the former being apparently the larger. This could be due to either of two factors, and probably both: first, the tissues of the juvenal wing are tender, and as a result the wing may dry with less angulation at the end of the metacarpus than occurs in older birds; second, the unworn juvenal primaries are more pointed than those of the adult. Whatever the explanation, the difference is clearly not a result of random variation since it shows up not only in both sexes of the Alaskan juveniles, but also in juveniles of both sexes collected in interior Canada. In the latter the difference is of lesser degree and the specimens represent individuals in migration averaging certainly several weeks older than the Alaskan juveniles.

In the five tables of mensural data for *L. scolopaceus*, magnitude of differences in wing length between adult and first-year birds fluctuates; partly because, by summer, specimens of all age groups vary so greatly in degree of wing-tip wear that the slight difference between age groups tends to be obscured (examine table 17, for example), and partly because the tables differ with respect to relative preponderance of specimens from certain seasons of the year. Thus, in table 6 the majority of the specimens were taken in March

and April, and the sample there summarized probably best indicates the magnitude of difference between adults and first-year birds. In table 7 the specimens are more scattered with respect to date of collection.

These variations, however, do not affect the basic value of the data. The main fact which tables 6, 7, 17, 18, and 19 establish is that there is a consistency in statistics derived from independent samples of *L. scolopaceus*. These results indicate that we are dealing with the same biological unit in different parts of its extensive distributional range. Migrant populations occurring on the Pacific coast, in the interior of North America and Mexico, and to a less extent on the Atlantic coast, are all derived from a breeding population, relatively restricted areally, in northern and western Alaska and probably also in extreme northern Yukon and northwestern Mackenzie.

ANALYSIS OF OTHER POPULATIONS OF LIMNODROMUS GRISEUS

BREEDING POPULATIONS

According to data available in the literature at present, the short-billed dowitcher is definitely known to breed only in interior Canada (see fig. 4, p. 35). From areas east of Hudson Bay there are a few summer-taken specimens, but no definite breeding records, and opinion differs concerning the probability of its nesting there. Evidence to be presented below clearly indicates that there is an eastern population of short-billed dowitchers, ignorance of its breeding range notwithstanding.

A third breeding area actually exists, the southern Alaskan coast, and the breeding or near-breeding specimens obtained there by several collectors have been considered erroneously to represent *L. scolopaceus*. It will be recalled that in his study of California dowitchers Orr (1940) reported the short-billed form five times more common than the long-billed form; although my data do not confirm this conclusion about the relative abundance of the two forms, they do demonstrate, as did those of Orr, that short-billed dowitchers are common on the California coast. Should all these be considered to have come from the breeding areas of interior Canada? On the basis of comparative data from interior Canada and California, the answer is No. As with respect to the eastern population, even if we knew nothing about an Alaskan population of the short-billed dowitcher, the data on Pacific coast short-bills would force us to the conclusion that these birds are in part at least derived from a population other than that of interior Canada.

Because the breeding status of the interior Canadian population is established beyond question, the analysis of distribution and racial variation in the species *griseus* as a whole may begin with that population. Mensural data from specimens collected in Alberta, Mackenzie, and Saskatchewan are given in table 20. These can be taken to represent the population named by Rowan (1932:22) as *L. griseus hendersoni*, the type locality of which is Devil's Lake, Alberta. Mensural data from specimens collected in Manitoba are given in table 21.

Comparison of tables 20 and 21 reveals that eastward in this interior population, there is a slight but significant decrease in wing size (see fig. 7, p. 39). In length of culmen the difference is near one millimeter, in itself insignificant (see fig. 8, p. 40); but the direction of difference, which agrees with that of wing length, is the same for both sexes.

Variation in color of under parts in the interior populations is shown in figure 5 (p. 36). It is evident there that practically all degrees of ventral

TABLE 20
MEASUREMENTS OF *LIMNODROMUS GRISEUS* FROM ALBERTA AND SASKATCHEWAN

Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	31	138-152	145.7 \pm 0.6	3.0	2.0
	♂ ♂	32	136-150	143.4 \pm 0.5	2.7	1.9
Culmen	♀ ♀	36	58.2-65.9	62.38 \pm 0.37	2.23	3.57
	♂ ♂	40	52.6-61.2	57.50 \pm 0.29	1.85	3.22
Tarsus	♀ ♀	37	35.3-41.3	37.93 \pm 0.24	1.45	3.82
	♂ ♂	41	33.8-39.3	36.71 \pm 0.20	1.31	3.57

TABLE 21
MEASUREMENTS OF *LIMNODROMUS GRISEUS* FROM MANITOBA

Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	28	137-147	142.5 \pm 0.5	2.5	1.8
	♂ ♂	23	135-142	139.6 \pm 0.5	2.1	1.5
Culmen	♀ ♀	37	56.2-67.8	61.33 \pm 0.44	2.74	4.47
	♂ ♂	35	50.8-61.1	56.73 \pm 0.40	2.38	4.20
Tarsus	♀ ♀	37	34.0-39.7	37.82 \pm 0.22	1.33	3.52
	♂ ♂	35	34.1-38.3	36.51 \pm 0.20	1.19	3.26

spotting are represented in these populations, but the noteworthy feature of the variation is the number of specimens with reduced amount of both spotting and whiteness. This reaches an extreme in the Alberta-Mackenzie-Saskatchewan population, as noted by Rowan (1932:22-23), in which specimens in spotting classes C, D, and E include 89 per cent of the total males and 83 per cent of the total females, and specimens in ground-color classes d and e include 67 per cent of the total males and 70 per cent of the total females. The corresponding figures for the Manitoba population are, for spotting, 59 per cent of the males and 72 per cent of the females, and, for ground color, 48 per cent of the males and 47 per cent of the females.

Mensural and ventral-color characters of the interior population may now

be compared with those of the Californian population (tables 8 and 22). No significant differences in statistics of culmen and tarsus occur, but the data on wing length strongly indicate that the Californian population includes, in fact consists chiefly of, individuals larger in wing length than is observed

TABLE 22

VARIATION IN COLOR OF UNDER PARTS IN POPULATIONS OF LIMNODROMUS GRISEUS

Population	Sex	+ Spotting -					Totals	+ Whiteness -				
		A	B	C	D	E		a	b	c	d	e
California.....	♀ ♀	32	27	20	4	3	86	3	30	46	7	0
	♂ ♂	16	31	22	14	4	87	0	23	49	12	3
Oregon, Washington, British Columbia.....	♀ ♀	8	11	7	2	0	28	1	4	14	6	3
	♂ ♂	6	5	15	7	1	34	1	4	14	13	2
Alaska.....	♀ ♀	8	4	2	0	0	14	0	4	5	4	1
	♂ ♂	5	4	7	1	1*	18	0	1	11	5	1
Alberta, Saskatchewan, Mackenzie.....	♀ ♀	1	4	15	4	6	30	0	1	8	16	5
	♂ ♂	0	3	14	5	5	27	0	4	5	9	9
Manitoba.....	♀ ♀	1	8	20	3	0	32	0	4	13	9	6
	♂ ♂	1	10	9	7	0	27	0	3	11	9	4
Eastern Canada, eastern New England coast....	♀ ♀	20	4	2	0	0	26	6	17	3	0	0
	♂ ♂	18	9	1	0	0	28	11	16	1	0	0
Southern New England coast, Long Island....	♀ ♀	18	5	1	0	0	24	4	13	5	2	0
	♂ ♂	6	1	2	0	0	9	1	7	1	0	0
Central Atlantic states (New Jersey-North Carolina).....	♀ ♀	28	11	11	1	0	51	12	24	4	8	3
	♂ ♂	41	6	4	3	3	57	25	15	8	6	3
South Atlantic states (So. Carolina-Florida)	♀ ♀	14	3	13	3	2	35	5	12	7	9	2
	♂ ♂	9	6	21	6	1	43	6	12	6	7	12
Gulf coast (Fla.-Texas)..	♀ ♀	0	2	4	2	1	9	0	1	0	5	3
	♂ ♂	0	2	2	9	2	15	0	0	3	7	5

* Immaculate; all others in class E showed obsolete spotting on breast, none on belly.

of the interior populations. As for ventral coloration in the Californian sample, only 46 per cent of the males and 31 per cent of the females occur in spotting classes C, D, and E; and only 17 per cent of the males and 8 per cent of the females occur in ground-color classes d and e.

In other words, even if the Californian population includes an occasional migrant or vagrant from interior Canada, which it probably does, that population is composed largely of birds which breed not within the known interior Canadian range, but somewhere else. Considering that an east-to-west

increase in wing length is observed within the interior Canadian populations, and taking into account also the geography of the situation, it seems reasonable to conclude that the large-winged Californian dowitchers may be derived from a breeding population occurring to the west of that of interior Canada.

TABLE 23
MEASUREMENTS OF *LIMNODROMUS GRISEUS* FROM ALASKA

Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	16*	145-155	150.3 \pm 0.7	2.9	1.9
	♂ ♂	17*	142-151	146.2 \pm 0.6	2.6	1.8
Culmen	♀ ♀	17†	56.6-67.7	62.18 \pm 0.63	2.60	4.18
	♂ ♂	24†	51.5-61.5	56.87 \pm 0.62	2.95	5.19
Tarsus	♀ ♀	17†	36.8-41.2	38.30 \pm 0.27	1.12	2.92
	♂ ♂	25†	33.4-40.0	36.70 \pm 0.32	1.56	4.25

* Adults only.

† Adults and first-year birds near one year of age.



Fig. 3. Distribution of *Limnodromus griseus caurinus* in southern Alaska. Dots indicate summer records; a square indicates type locality; triangles indicate migrant records. All solid symbols represent specimen records; a circle indicates a record from literature. Actual breeding known only near Yakutat (type locality) and on the mainland at Bristol Bay.

Data on available Alaskan specimens, first segregated according to color characters described on pages 7-10, are given in tables 22 and 23. Comparison of these previously cited data shows that the Alaskan population shares the size and color characters of the Californian population.

When localities represented by Alaskan specimens of *L. griseus* are plotted on a map (see fig. 3), it is seen that they are limited to the southern coast and peninsula and thus occupy an area in which *L. scolopaceus* is not known to breed. Were the populations of Alaskan dowitchers those of a single, highly variable race, as some students maintain, this result would not be possible and some specimens in my sample of 47 Alaskan short-bills would have had

to turn up within the range of *scolopaceus* to the north. Conversely, breeding specimens of *scolopaceus* would be expected from the area here ascribed to *griseus*, but I have seen none; and specimens identified as *scolopaceus* actually represent *griseus*.

The several conclusions to be drawn from the foregoing evidence are (1) that Californian short-billed dowitchers represent migrants of an Alaskan breeding population; (2) that this population is racially distinct from the interior Canadian population, differing in size of wing and in ventral coloration; and (3) that *griseus*, like *scolopaceus*, breeds in coastal parts of Alaska,

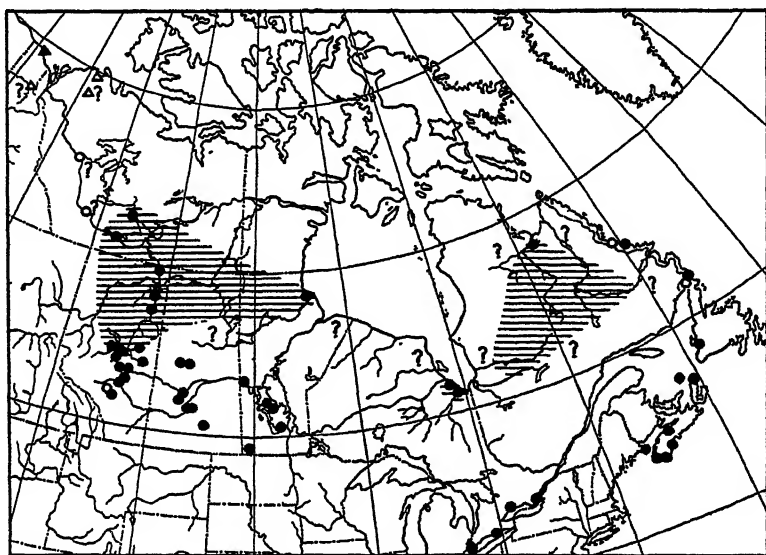


Fig. 4. Distribution of *Limnodromus griseus* in Canada. Area of parallel lines in interior Canada indicates known breeding range of *L. g. hendersoni*; that on the Ungava Peninsula indicates probable breeding range of *L. g. griseus*; that on James Bay may represent *L. g. griseus* or an intergrade population. Solid dots represent specimen records; circles represent important locality records selected from the literature. A solid triangle in northern Yukon indicates the easternmost specimen record of *L. scolopaceus* on the Arctic coast; three hollow triangles indicate localities recorded in the literature tentatively assigned to *L. scolopaceus* (see fig. 2).

but their respective ranges are complementary, *scolopaceus* occurring in northern and western Alaska, *griseus* in southern Alaska.

Before a formal description of the Alaskan population of *L. griseus* is given, it is necessary to examine evidence from the eastern population previously mentioned, inasmuch as Conover (1941) and Aldrich (1948) have considered Pacific coast specimens of the short-billed dowitcher to represent *L. g. griseus* at the same time that they recognized the interior race *L. g. hendersoni*. Specimens from the Ungava Peninsula are too few for statistical treatment. The best source of data on a possible eastern breeding population is the specimens obtained on the Atlantic coast from Massachusetts northward. The map of eastern North America (fig. 4) shows that these specimens, totaling more than

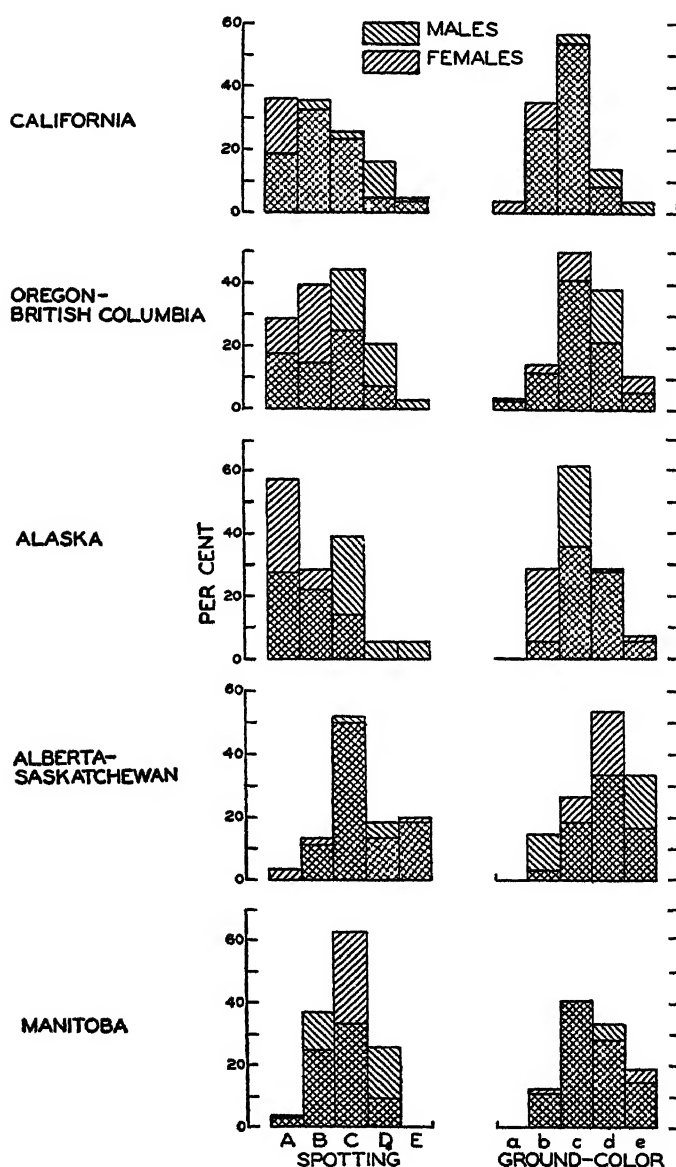


Fig. 5. Superimposed percentage frequency distributions of males (100 per cent) and females (100 per cent) in spotting classes A-E and ventral ground-color classes a-e in populations of *Limnodromus griseus* along the Pacific coast, in Alaska, and in interior Canada. Original data in table 22.

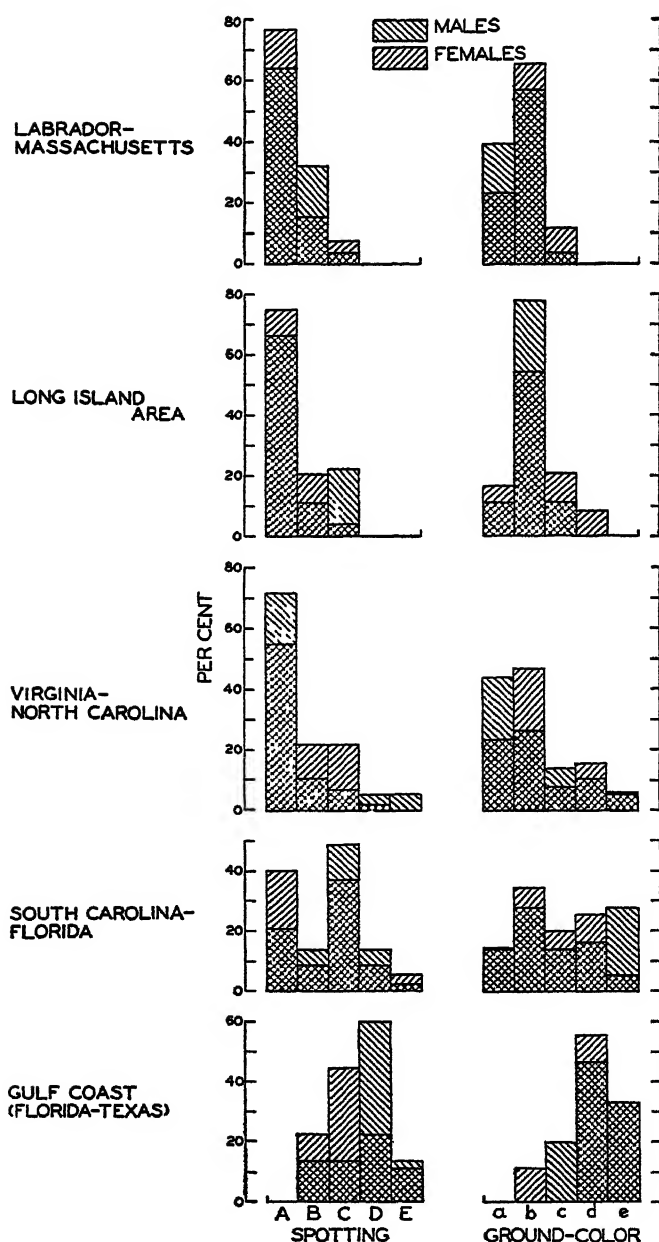


Fig. 6. Superimposed percentage frequency distributions of males (100 per cent) and females (100 per cent) in spotting classes A-E and ventral ground-color classes a-e in populations of *Limnodromus griseus* along the Atlantic and Gulf coasts. Original data in table 22.

a hundred, may be assumed to represent individuals which, if they are really in migration, are probably moving toward or away from a breeding area other than interior Canada; whereas migrant populations on Long Island Sound and more southern portions of the Atlantic coast may (and do; see page 45) include individuals from interior Canada.

The data provided by the northeastern population just defined have been combined with those from a few specimens from Labrador, Quebec, and eastern Ontario and are summarized in tables 22 and 24. In ventral colora-

TABLE 24
MEASUREMENTS OF LIMNODROMUS GRISEUS FROM THE ATLANTIC COAST OF CANADA
AND NEW ENGLAND SOUTH TO MASSACHUSETTS

Dimension	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	♀ ♀	Adult.....	22	136-144	140.4 ±0.5	2.2	1.6
		Juvenal.....	19	137-147	141.2 ±0.7	2.9	2.1
	♂ ♂	Adult.....	22	133-145	138.8 ±0.7	3.3	2.4
		Juvenal.....	30	133-147	139.3 ±0.7	3.7	2.7
Culmen	♀ ♀	Adult and first-year..	25	56.4-63.3	58.78±0.52	2.60	4.42
		Juvenal.....	19	53.9-65.1	59.95±0.72	3.14	5.24
	♂ ♂	Adult and first-year..	35	51.2-60.4	55.16±0.32	1.87	3.39
		Juvenal.....	30	52.0-61.1	56.08±0.47	2.41	4.30
Tarsus	♀ ♀	Adult and first-year..	27	31.3-37.3	34.35±0.26	1.37	3.99
		Juvenal.....	19	33.0-39.5	35.76±0.38	1.66	4.64
	♂ ♂	Adult and first-year..	35	31.5-35.7	33.77±0.17	0.98	2.90
		Juvenal.....	29	32.0-38.9	35.23±0.32	1.62	4.60

tion, only 3.6 per cent of the males and 7.7 per cent of the females fall into spotting classes C, D, and E; no specimen falls into ground-color categories d and e. These results are obtained from first-year and adult birds together, and they do not differ if adults, so far as these can be separated, are considered alone. In other words, contrary to Brodtkorb (1933:127), the heavy spotting and extensive white coloration of under parts of dowitchers are not indicative of "one-year old birds," and significant geographic variation in spotting and ground color does occur.

In ventral coloration the northeastern population contrasts strikingly with that of interior Canada, the former being much more spotted and white. As shown by figures 5 and 6, the Manitoba population tends toward the eastern form in these characters, but only slightly so. It is most similar to the Alberta-Mackenzie-Saskatchewan population.

As is shown by table 22 and figure 6, in ventral coloration the eastern population and the Alberta-Saskatchewan population prove to be the extremes

in the species as a whole. The Alaskan population consists of individuals approaching or reaching both extremes and others of varying intermediacy in ground color, spotting, or both. It is clear now why certain Pacific coast specimens were linked with the eastern population if color alone is considered.

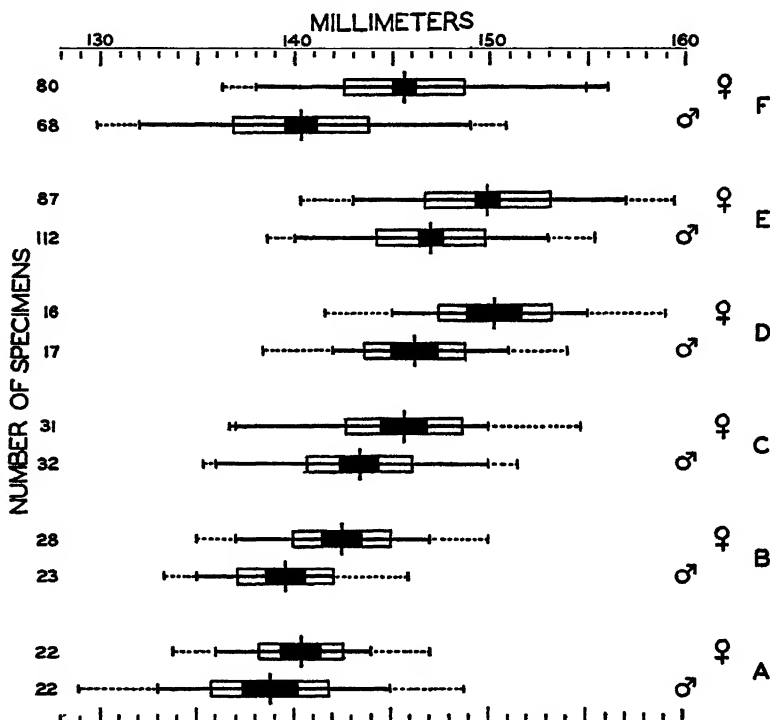


Fig. 7. Variation in size of wing in populations of *Limnodromus griseus* (A-E) and *L. scolopaceus* (F). A, eastern Canada and New England coast north of Cape Cod (table 24); B, Manitoba (table 21); C, Alberta and Saskatchewan (table 20); D, Alaska (table 23); E, California (table 8); F, California (table 7). In each diagram, the mean is marked by a vertical line; a rectangle to either side indicates standard deviation (σ); dark part of each rectangle indicates twice standard error of mean; observed range of variation is shown by a solid line; limits of 3σ to either side of mean, beyond observed range, is shown by a broken line. The observed upper limit in females of *L. scolopaceus* exceeds $M + 3\sigma$. For a discussion of the use of this method in demonstrating differences between populations and their significance see Hubbs and Perlmutter (1942).

In size, the eastern dowitchers (table 24, figs. 7-9) prove to be the smallest in this species and so extend further the east-west trend already indicated for the interior and Alaskan populations. It has already been shown that first-year and adult birds do not differ in size of culmen and tarsus, and the means of these dimensions in the eastern population differ significantly from those in the other populations. Thus, it is conclusively evident that age variation does not enter into the color distinctions drawn above between the eastern and interior populations. If age variation did so enter, the mensural differences just described could not exist.

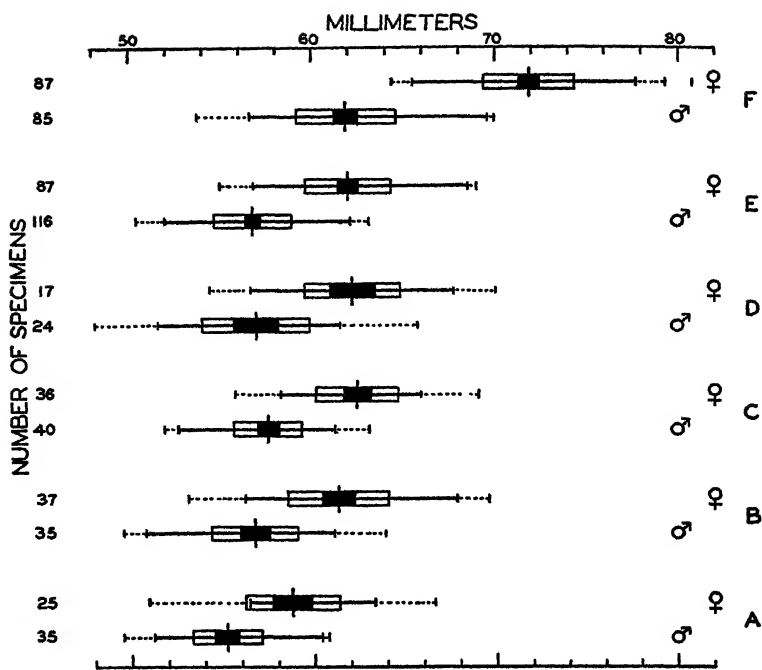


Fig. 8. Variation in length of culmen. See legend of figure 7 for explanation. One observation among females of *L. scolopaceus* exceeds $M + 3\sigma$.

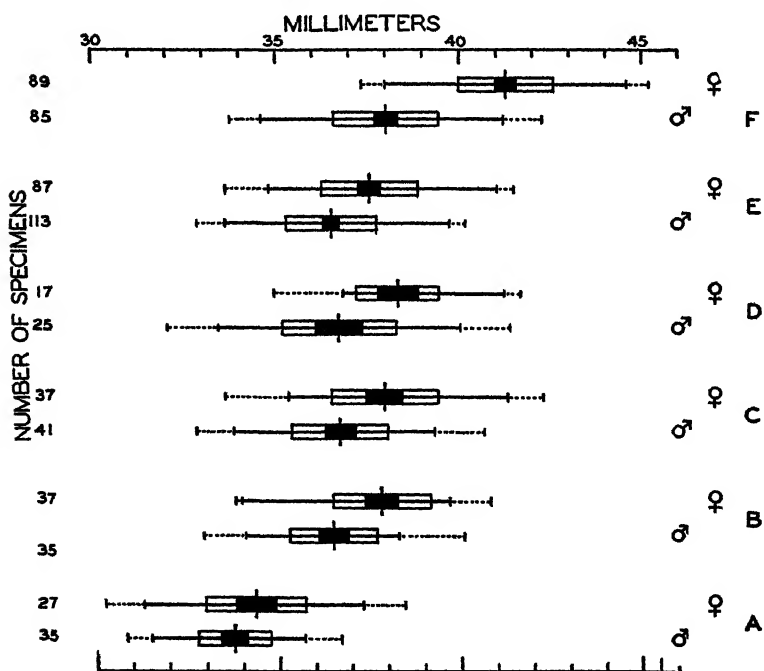


Fig. 9. Variation in length of tarsus. See legend of figure 7 for explanation.

From the foregoing evidence we may conclude that the assumption about the migrational relations of dowitchers collected along the coasts of Canada and New England south to Massachusetts, ventured at the outset of this section, is valid and that adult specimens and most juveniles and first-year birds collected there represent a population distinct from that of interior Canada and Alaska.

Mention may be made at this point of color of the dorsum. It does not vary so as to provide characters serving to separate the three races, a fact already recognized by Conover (1941:379) in his comparison of *L. g. griseus* and *L. g. hendersoni*. Nevertheless, such variation as is evident reflects the differences which occur in color of under parts. The edgings of unworn dorsal feathers in the eastern population (*L. g. griseus*) average grayer (less buff) and somewhat narrower than those in the interior populations (*L. g. hendersoni*). In the eastern population, it appears that the nuptial plumage is assumed at an earlier average date than in the interior population; because of this, and because the gray or buff edgings of dorsal feathers are narrower, the back becomes dark through feather wear in *griseus* at a time when the buff edges are still conspicuous in *hendersoni*. Individuals of *L. g. griseus* which underwent the prenuptial molt early in spring are exemplified by a male collected at St. Croix, Virgin Islands, on March 18, 1940 (CM 158030), which appears to be in a late stage of that molt. A male collected at the same place on April 20, 1940 (CM 158035), already shows some wear of dorsal feathers although a few lateral breast feathers of the nuptial plumage are not fully grown (sheathed basally). Specimens of *L. g. griseus* in migration, collected in the first half of May (for example, CM 133871, May 14, 1901, and CM 133887, May 8, 1902, both from Pea Island, North Carolina) show considerable wear of back feathers. In the Pacific coast populations, as with ventral color, variation in dorsal color characters includes extremes of both *griseus* and *hendersoni* indicated above.

One consideration remains. Table 24 reveals means in all dimensions of both sexes of juvenal specimens slightly larger than the corresponding means for older birds. Coefficients of variation are consistently larger in the former groups. Most of the "juvenal" specimens which provided the data given in table 24 were collected from Nova Scotia to Cape Cod in August and September. It seems reasonable to explain the results just cited as caused by an ingressive eastward movement of young-of-the-year from the breeding range of the larger race of interior Canada, *L. g. hendersoni*. As will be shown later, this race apparently occurs regularly from Chesapeake Bay southward and rarely farther north (see table 26, p. 46). It is not surprising, therefore, to detect the presence of more freely wandering young birds in their first fall migration even farther north on the Atlantic coast.

In summary, three racially distinct breeding populations of *Limnodromus griseus* are to be recognized: *L. g. griseus* (Gmelin), *L. g. hendersoni* Rowan, and an unnamed Alaskan race.

L. g. griseus presumably breeds on the Ungava Peninsula (fig. 4). There are but three specimens collected north of Ontario and Newfoundland: an

adult female taken near Fort Chimo in northern Quebec (US 94471), probably a breeding individual (see Aldrich, 1948), and two juveniles collected on the Labrador coast. One of the latter collected at Turnavik West by Gross (1937:25) was taken from a flock of four individuals. The other, collected by Coues (1861:229), at Henley Harbor, was a lone individual. Turner (1885:246), who collected the specimen from Fort Chimo, also obtained one at Davis Inlet (see Austin, 1932:101). One wonders what evidence Turner (*loc. cit.*) had when he stated that dowitchers were "common in southern and western portions," since the territory on which he was reporting included the whole of the Ungava Peninsula north of 50° latitude.

A male specimen collected by C. E. Hope on the Nettichi River just south of Fort Albany on James Bay, on July 16, 1942, is similar to and was included among eastern Canadian specimens (table 24). The label of this specimen (ROM 67901), an adult male, bears the notation, "agitated bird, possessed well-defined incubating patches on breast." The indications are that this was a breeding individual and that *Limnodromus griseus* may be sought as a breeding species in the James Bay area. Such a population might prove to connect the interior race *hendersoni* with the eastern race *griseus*.

Another specimen from the same area, an adult female collected on May 17, 1930, at Moose Factory (ROM 33620286), may represent an intergrade between *griseus* and *hendersoni* (as indeed may be true of the Nettichi River specimen), or it may be a migrant of *hendersoni*. The ventral color of this specimen, excluded from table 24, is Cc (table 1); its dimensions are: wing 148 mm., culmen 60.7, and tarsus 37.0.

The scarcity of specimens from eastern Canada does not deter me from the conclusions already drawn. The data on size and color characters, establishing as they do the existence of an eastern population of dowitchers distinct from that of interior Canada, far outweighs, in my opinion, the negative evidence from the few published distributional records. Moreover, the good number of specimens obtained from better known parts of the Atlantic coast from Cape Cod north to Newfoundland indicates that the paucity of specimens from Ungava is most likely due to the paucity of field work in that vast area.

L. g. hendersoni breeds from the western coast of Hudson Bay (Churchill, Manitoba) westward to central Alberta (Fawcett, Klondike City, and Rochester; see Rowan, 1932:15) and possibly east-central British Columbia (Tupper Creek, Peace River District; see Cowan, 1939:31), north to Great Slave Lake (Big Island, Fort Rae). Records from Fort Simpson and Fort Norman (Preble, 1908:319), while now listed tentatively under *L. scolopaceus*, may apply to *hendersoni* (see fig. 4). *L. g. hendersoni* probably breeds in northern Saskatchewan and parts of northern Manitoba and southern Mackenzie other than those recorded above, but no records are available. There are several June-taken specimens from south-central Saskatchewan (Montreal Lake, Osler, Last Mountain Lake) and southern Manitoba (Lake St. Martin, Hal-crow Lake), but the dowitcher is not definitely known to breed in these areas. (See Shortt and Waller, 1937:23, however, for evidence of breeding at Lake St. Martin.)

The unnamed race of *L. griseus* which breeds in southern Alaska may be known as *Limnodromus griseus caurinus*, new subspecies.

Type.—Female, number 36.9.18.25 Royal Ontario Museum of Zoology, collected at Yakutat, southeastern Alaska, May 21, 1936, by T. M. Shortt; field number 85; "contained egg almost ready for laying." (See Shortt, 1939:15, where date of collection of specimen selected as type should read May 21, not 29.) The type is one of a series (pl. 2) obtained by Shortt, who states (letter): "The birds collected . . . were in migrating flocks . . . of 10 to 20 that were moving along the coast." However, Shortt found dowitchers "summering in the muskegs near the Situk River" (*loc. cit.*), just east of Yakutat.

Diagnosis.—Largest of the three races of *Limnodromus griseus* (see figs. 7-9). Average dimensions of females: wing 150.3 mm. (σ , 2.9), culmen 62.18 mm. (σ , 2.60), tarsus 38.30 mm. (σ , 1.12). Percentage differences between females of *caurinus* and those of other races:

	<i>L. g. hendersoni</i>		<i>L. g. griseus</i>
	Alberta, etc.	Manitoba	
Wing	-3.1	-5.2	-6.6
Culmen	+0.3	-1.4	-5.5
Tarsus	-1.0	-1.3	-10.3

Characterized, as a population, by a preponderance of individuals with moderate to heavy spotting on under parts and presence of white on mid-belly, less often on entire belly (see fig. 5); thus, compared with *hendersoni*, more heavily and densely spotted and more white ventrally; compared with *griseus*, more varied in ventral coloration (since color variants of "*hendersoni*" type occur in *caurinus*), not so heavily spotted nor so white ventrally; averages intermediate between *hendersoni* and *griseus* in ground color, but closer to *griseus* than to *hendersoni* in spotting.

Distribution.—The known breeding range of the Alaskan short-billed dowitcher lies in southern Alaska, along the mainland coast from Nushagak Bay east to Yakutat Bay (fig. 3). A series of summer-taken specimens, in both breeding and juvenal plumages, is available from the Alaskan Peninsula, the outermost locality being Izembek Bay near the peninsula tip; however, it is not known at present whether these represent breeding populations. Some of them, at least, are probably local migrants. Also, a breeding record from Goodnews Bay, west of Nushagak Bay (see p. 25), may apply to *L. g. caurinus*.

There are no Alaskan specimen records of *Limnodromus griseus caurinus* north and west of Kenai and Nushagak. In southeastern Alaska, south of Yakutat Bay, the known localities of migrant occurrence, obtained from 22 specimens, are as follows: Caamano Point, Craig, Hooniah Sound, 22 miles north of Juneau, Kuiu Island, and mouth of the Stikine River, April 26-May 16, which are inclusive dates for 21 specimens; one juvenile from Kruzoff Island was taken on August 17, 1913.

MIGRANT AND WINTERING POPULATIONS

L. g. griseus occurs in migration chiefly along the Atlantic coast, on the Bahama Islands and Lesser Antilles south to the coast of Brazil (Mangunca I., Maranhão; Recife). It winters probably chiefly in the eastern Caribbean area, as is indicated by the fact that most specimens unequivocally representing the race *griseus* come from that area. Its occurrence to the west of Florida cannot be determined except from extreme specimens because of the overlap of dimensional characters between *griseus* and *hendersoni*, and but one such specimen is available, a first-year male collected on Deer Island, Mississippi, November 5, 1940 (BS 363739), wing 133 mm., culmen 56.1, and tarsus 33.0.

L. g. hendersoni occurs as a migrant through the Mississippi Valley and along the Atlantic coast, occasionally north to New Hampshire (see table 26)

and commonly from Chesapeake Bay south over the Caribbean area probably to the northern and northwestern coasts of South America. Again because of overlap in dimensional characters between *hendersoni* and both *griseus* to the east and *caurinus* to the west, and also because of the paucity of specimens, precise definition of winter range is not possible. A juvenile male from Perme, Panama (MCZ 155090), collected October 25, 1929, appears

TABLE 25
MEASUREMENTS OF LIMNODROMUS GRISEUS FROM THE ATLANTIC AND GULF COASTS

Dimension	Sex	Location	Number of specimens	Range	Mean with standard error	Standard deviation
Wing	♀ ♀	Long Island.....	19	138-150	143.0 ±0.7	2.9
		Va.-N. C.....	53	138-152	145.4 ±0.4	2.9
		S. C.-Florida....	49	137-150	144.3 ±0.4	2.7
		Gulf coast.....	19	134-153	144.1 ±0.9	4.0
	♂ ♂	Long Island.....	10	135-145	140.3 ±1.1	3.5
		Va.-N. C.....	50	134-149	141.5 ±0.5	3.9
		S. C.-Florida....	56	133-151	141.3 ±0.6	4.2
		Gulf coast.....	22	135-147	142.2 ±0.7	3.5
Culmen	♀ ♀	Long Island.....	24	56.5-64.6	59.73±0.43	2.11
		Va.-N. C.....	67	55.5-69.0	61.44±0.36	2.94
		S. C.-Florida....	66	54.8-68.1	61.61±0.33	2.71
		Gulf coast.....	39	55.0-66.8	61.06±0.49	3.05
	♂ ♂	Long Island.....	13	51.0-61.3	56.23±1.01	3.62
		Va.-N. C.....	71	50.5-63.2	56.17±0.31	2.58
		S. C.-Florida....	73	52.0-64.0	57.26±0.29	2.55
		Gulf coast.....	41	51.4-61.0	57.09±0.32	2.03
Tarsus	♀ ♀	Long Island.....	26	31.3-37.5	35.04±0.29	1.50
		Va.-N. C.....	69	31.6-39.8	36.08±0.22	1.86
		S. C.-Florida....	67	32.4-40.0	36.16±0.18	1.50
		Gulf coast.....	39	33.6-39.3	37.06±0.29	1.79
	♂ ♂	Long Island.....	13	31.6-38.4	34.15±0.56	2.04
		Va.-N. C.....	71	31.2-38.7	34.43±0.21	1.78
		S. C.-Florida....	73	31.9-40.2	35.70±0.21	1.77
		Gulf coast.....	41	34.2-38.9	36.18±0.17	1.10

to represent *hendersoni* (wing 137 mm., culmen 56.5, tarsus 37.4). Dimensions of a juvenal male from Pizarro, Choco, on the Pacific side of Colombia (HBC 16476), fall into the overlap between *hendersoni* and *griseus* (wing 139 mm., culmen 54.9, tarsus 33.0), but the specimen probably represents a small variant of *hendersoni*. This race occurs as far east in the Caribbean area as peninsular Florida and the Bahama Islands (see table 26).

Among specimens taken along the Atlantic and Gulf coasts, races of *L. griseus* can be determined to a satisfactory degree because of the marked

size and breeding-plumage distinctions between *hendersoni* and *griseus*. For purposes of analysis of the large mass of available data, the Atlantic coast has been divided arbitrarily into four segments: the northeast coast north of Cape Cod; the southern New England coast and Long Island; the central coast from New Jersey to North Carolina, and the southern coast from South Carolina to Florida. That these segments are not roughly equivalent in linear distance does not matter. The data on variation in breeding plumage are given in table 22 and figure 6; those on mensural characters, in tables 24 and 25.

These data show that southward to Florida and thence on the Gulf coast, numbers of specimens in spotting classes C, D, and E and in ground-color classes d and e increase, at least relatively. Comparison of dimensions of the geographically successive samples from the Atlantic and Gulf coasts with those from interior Canada (tables 20 and 21) reveals progressive increase in size from typical *L. g. griseus* on the eastern Canadian coast to *L. g. hendersoni* on the Gulf coast. Thus, data from both color and dimensional characters demonstrate that *hendersoni* occurs as a migrant on the Atlantic coast. This fact has already been pointed out by Aldrich (1948), who, however, provided no supporting evidence.

Atlantic coast records were examined for specific occurrences of the race *hendersoni*, and for this purpose the following criteria were adopted: A specimen was identified as *hendersoni* when (1) it fell into spotting classes C, D, or E (see table 1), or (2) when it was placed in ground-color classes d or e, or (3) when two of the three dimensions taken were as follows:

Females: wing 148 mm. or more, culmen 63 mm. or more, tarsus 39 mm. or more.

Males: wing 146 mm. or more, culmen 61 mm. or more, tarsus 37 mm. or more.

Examination of table 22 and comparison of tables 20, 21, and 24 will show ample statistical justification for these criteria. In the majority of specimens, both color and mensural extremes were those of *hendersoni*. There is, of course, the possibility that a few of the specimens so identified may represent extreme variants of *griseus*. To eliminate these at least partially, individuals in spotting class C, but in ground-color classes a, b, or c and of dimensions smaller than those given above, were omitted.

The total number of specimens identified as *hendersoni* was 122. Localities and dates of occurrence for these specimens are given in table 26. Obviously, many additional specimens, falling into the overlap zone between *hendersoni* and *griseus*, must represent the former race. Thus, even allowing for a small error in the figure of 122, it is conclusively evident that *hendersoni* is a relatively common migrant on the Atlantic coast.

All records of *hendersoni* from New York northward (table 26) are summer or fall occurrences. The three July records apparently represent nonbreeding individuals, two and possibly all of which are first-year birds. These three records do not appear in a listing of records of nonbreeding individuals of *L. griseus* as a whole (table 28), to be considered later, because by early July *L. g. griseus* appears on the Atlantic coast of the United States in migration,

TABLE 26
ATLANTIC COAST OCCURRENCES OF *L. G. HENDERSONI*

State or Islands	Locality	Date
New Hampshire...	Rye Beach.....	Aug. 27
Massachusetts....	Chatham.....	Aug. 25
	East Orleans.....	Sept. 14
	Monomoy I.....	Sept. 12
	Newburyport.....	July 23
Rhode Island.....	Newport.....	Aug. 10
Connecticut.....	Guilford.....	Aug. 27
New York.....	East Rockaway.....	Sept. 16
	Good Grounds.....	July 12, 19
	Oak Beach Flats.....	Aug. 28
	Rockaway.....	Sept. ?
New Jersey.....	Cape May.....	May ?
Virginia.....	Bono I.....	July 14 (2)
	Cape Charles.....	May 12
	Cobb I.....	July 20 (2), 29; Sept. 6
	Smith I.....	Aug. 24
	Wachapreague.....	Aug. 25
North Carolina...	Bodie I.....	April 25, 26
	Cape Fear.....	July 7
	Currituck Light Beach.	Aug. 2 (3)
	Hatteras.....	March 4 (2); Aug. 4; Sept. 10
	New Inlet.....	July 8, 11 (2)
	Pea I.....	May 6, 13; July 8, 11 (4), 15
	Swannanoa.....	July 5
South Carolina....	Bird Key.....	Nov. 14
	Bull's Bay.....	Oct. 31 (2)
	Charleston.....	July 22; Sept. 10
	Christchurch Parish....	May 2 (3), 5
	Copahee Sound.....	April 30 (2); May 2, 3, 6 (2), 14 (2), 21; July 13, 19, 20; Aug. 11
	Dewee's I.....	Feb. 6
	Fripp I.....	Aug. ?
	Frogmore.....	April 27; May 5 (2)
	Mount Pleasant.....	Jan. 23, 24; April 29; May 3, 18; Aug. 5; Sept. 11 (2), 23
	Porcher's Bluff.....	May 2
	Price's Inlet.....	May 7
	Seabrook I.....	May 26
	Sullivan's I.....	May 13 (2), 17; Aug. 13 (2)
	Wayne's Place.....	April 28, 29 (2); May 2 (4), 3; Nov. 14

TABLE 26—Continued

State or Islands	Locality	Date
Georgia.....	Chatham County.....	May 16
	Savannah.....	April 24 (2)
Florida.....	Amelia I.....	March 5 (2)
	Cape Sable*.....	May 4 (2)
	Caxambox*.....	May 7
	Cedar Keys*.....	May 13 (2), 14, 16, 17 (2)
	Clearwater*.....	July 19
	Gulfport*.....	March 23
	Key West.....	Feb. 1
	Marco*.....	July ?
	Peninsula Point.....	May 11
Bahama Islands...	St. Marks*.....	April 27 (3)
	Andros I.....	April 28, 29; Nov. 25

* Gulf coast localities on peninsular Florida.

and therefore, among summer-taken specimens in breeding plumage, only those collected in June were regarded as probably bona fide nonbreeders.

Nine records for August and September from New York northward (table 26) are without exception those of juvenal birds. Here is added evidence that young-of-the-year of *hendersoni* account for the anomalously larger dimensions in the juvenal class of table 24 (see page 38).

The procedure used to segregate Atlantic coast specimens of *hendersoni* was also applied to *L. g. griseus*. A specimen was identified as *griseus* when (1) it fell into spotting class A in combination with (2) ground-color classes a or b, or (3) when wing or tarsus dimensions were as follows: females, wing 136 mm. or less, tarsus 33 mm. or less; males, wing 134 mm. or less, tarsus 32 mm. or less. Here again, for the majority of specimens, the evidence from color characters was confirmed by evidence from dimensional characters.

A total of 187 specimens were identified as *L. g. griseus*. Since there is nothing unexpected about the Atlantic coast occurrences of that race, a tabulation of them is not given, but the two totals obtained may be scrutinized.

I do not regard the figures 187 and 122 as indexes to the relative frequency of the two Atlantic coast races. In the first place, the approach in dimensions of the Manitoba population (table 21) toward *griseus* restricts the segment of the lower end of the size range wherein specimens may be assumed to represent *griseus*. Secondly, color variation is greater in the interior population than in the eastern population, and this has the same restrictive effect on the criteria set up for *griseus*. It is therefore evident that, relative to the total of 122 *hendersoni*, the total of 187 *griseus* should be larger if it is to reflect the degree to which *griseus* outnumbers *hendersoni*. Almost all former collectors on the Atlantic Coast have taken specimens without realizing that two races of the short-billed form were present; but some selection of ven-

trally buffy, unspotted specimens, favoring *hendersoni*, probably occurred. A number of authors have identified such specimens as long-billed dowitchers. From these considerations and the available data, I would hazard the guess that *griseus* outnumber *hendersoni* roughly 2 or 3 to 1 on the central and southeast Atlantic Coast and that from Chesapeake Bay northward this ratio increases rapidly. It may be of interest to recall that, on the basis of specimen evidence, *griseus* and *hendersoni* together outnumber *scolopaceus* on the Atlantic coast about 10 to 1.

Probably the main mass of the population of *L. g. hendersoni* migrates through the Mississippi Valley and eastward across the Great Lakes to the central Atlantic coast; but it is possible that some migratory movement of this race may occur through the Great Basin. However, to the west of the Dakotas, Nebraska, and eastern Texas I have seen but one specimen of *hendersoni*, an adult male collected at the mouth of the Bear River, Great Salt Lake, Utah, on May 20, 1915 (BS 261161).

To the immediate east of the Cascade-Sierra axis, only a few specimens of *L. griseus* have been collected, and as a group these represent *L. g. caurinus*. Data on wing length and plumage type of ten specimens from interior British Columbia (Osoyoos and Osoyoos Lake) are:

♀ Ce, 149 mm.	♀ Bc, 146 mm.
♀ Ac, 149 mm.	♂ Cd, 146 mm.
♀ Ab, 148 mm.	♂ Ec, 145 mm.
♀ Bc, 147 mm.	♂ Cd, 141 mm.
♀ Ce, 148 mm.	♂ Bc, 146 mm.

In wing length, all but one of these specimens fall between the means of the respective sexes of *caurinus* and *hendersoni*. The color variants include two (Ac and Ab) relatively rare in *hendersoni*, and two (Cd, Ec) relatively rare in *caurinus*. The eleventh specimen, taken in Imperial County, California (MVZ 71402), is an adult male and represents *caurinus* (plumage type, Ab; wing, 147 mm.; tarsus, 38.0). The twelfth, from El Dorado County, California (CAS 58071), is a male, apparently a first-year, nonbreeding individual, collected July 4, 1923, at Lake Tahoe; it is without decisive characters and could represent either *caurinus* or *hendersoni*. (See table 30, p. 54, where this specimen and the one from Utah are listed together.)

L. g. caurinus occurs as a migrant along the Pacific coast south probably to the coasts of Ecuador (Esmeralda, Vaqueria) and Peru (Vegeta). The excellent series of specimens available from the Pacific states agree in dimensions and color characters with those from Alaska; but from more southern parts of the Pacific coast, only a limited number of specimens is available. The few that have unworn wing tips or some indications of summer-plumage characters are more or less equivocal between *caurinus* and *hendersoni*.

Although it has not proved possible to define the winter ranges of the individual races of *L. griseus*, the excellent data from the Atlantic and Pacific coasts of the United States, together with the scattered records from Central America, the Caribbean area, and northern South America (see table 27), permit the following tentative statements: *L. g. griseus* migrates through

TABLE 27

CENTRAL AMERICAN AND SOUTH AMERICAN SPECIMENS OF LIMNODROMUS EXAMINED

Specimen no.	Sex	Location	Date	Culmen	Wing	Tarsus
<i>L. griseus (hendersoni or caurinus)</i>						
AM 173154*	♂	Tembleque I., Ecuador..	18 July '22	61.1	138	35.7
AM 173155*	♂	Tembleque I., Ecuador..	18 July '22	59.4	143	36.6
AM 173156*	♂	Tembleque I., Ecuador..	18 July '22	59.3	136	35.3
ROM 6322†	♂	Vaqueria, Ecuador.....	23 Aug. '01	61.3	143	35.6
MCZ 155090	♂	Perme, Panama.....	29 Oct. '25	56.5	137	37.4
AM 389081	♂	Guanacaste, Costa Rica..	1 Feb. '24	59.7	142	38.7
AM 389082	♂	Guanacaste, Costa Rica..	1 Feb. '24	61.0	147	36.1
AM 389083	♂	Guanacaste, Costa Rica..	8 Feb. '24	56.6	142	35.3
CM 74638	♂	Guanacaste, Costa Rica..	28 Jan. '24	60.9	149	37.2
CM 74640	♂	Guanacaste, Costa Rica..	3 Feb. '24	59.6	141	38.3
CM 74642	♂	Guanacaste, Costa Rica..	8 Feb. '24	58.1	142	36.8
HBC 2203	♂	Guanacaste, Costa Rica..	1 Feb. '24	53.7	145	35.8
HBC 2204	♂	Guanacaste, Costa Rica..	1 Feb. '24	59.8	144	38.8
HBC 2206	♂	Guanacaste, Costa Rica..	1 Feb. '24	56.2	140	36.1
CM 157984	♂	Pt. Jimenez, Costa Rica..	5 Dec. '29	58.7	144	36.5
CM 157985	♂	Pt. Jimenez, Costa Rica..	5 Dec. '29	60.2	141	37.5
DC 16742	♂	El Salvador.....	31 Dec. '25	57.8	144	36.7
DC 16743	♂	El Salvador.....	31 Dec. '25	59.6	141	36.0
DC 16971	♂	El Salvador.....	16 Jan. '26	54.2	141	37.2
DC 16970	♂	El Salvador.....	16 Jan. '26	53.6	141	34.4
DC 16973	♂	El Salvador.....	16 Jan. '26	57.2	138	36.6
CM 111238	♂	El Salvador.....	16 Jan. '26	57.7	141	35.7
AM 173157*	♀	Tembleque I., Ecuador..	18 July '22	65.3	151	38.3
AM 740385†	♀	Vaqueria, Ecuador.....	3 Aug. '01	55.9	141	34.7
AM 740386*	♀	Vaqueria, Ecuador.....	18 Aug. '01	65.0	145	37.1
AM 740387*	♀	Vaqueria, Ecuador.....	29 Aug. '01	58.5	138	36.0
AM 357159*	“♂” §	Vaqueria, Ecuador.....	3 Aug. '01	63.3	140	39.0
AM 357160	♀	Vaqueria, Ecuador.....	31 Aug. '01	61.5	139	38.4
AM 357161	♀	Vaqueria, Ecuador.....	31 Aug. '01	60.1	143	36.2
AM 357162	♀	Vaqueria, Ecuador.....	4 Sept. '01	61.5	142	37.3
ROM 6323†	♀	Vaqueria, Ecuador.....	30 July '01	63.2	...	36.9
ROM 6324†	♀	Vaqueria, Ecuador.....	25 Aug. '01	57.0	138	37.8
ROM 6339¶	♀	Vaqueria, Ecuador.....	3 Aug. '01	57.6	...	37.3
AM 118407	♀	Esmeraldas, Ecuador....	21 Oct. '12	62.1	142	36.7
PA 115836	♀	Peru.....	3 Feb. '32	63.4	145	38.3
CM 74639	♀	Guanacaste, Costa Rica..	30 Jan. '24	61.4	147	38.3
CM 74641	♀	Guanacaste, Costa Rica..	3 Feb. '24	57.4	142	38.4
HBC 2202	♀	Guanacaste, Costa Rica..	1 Feb. '24	64.0	146	39.7
HBC 2205	♀	Guanacaste, Costa Rica..	3 Feb. '24	65.8	147	39.9

* Summer-taken, nonbreeding specimens in winter plumage.

† Specimens in juvenal plumage, indicating early arrival from breeding grounds.

‡ In breeding plumage.

§ Incorrectly sexed? This is a nonbreeding specimen in winter plumage, with worn juvenal rectrices.

¶ Worn.

|| Mixed plumage.

TABLE 27—Continued

Specimen no.	Sex	Location	Date	Culmen	Wing	Tarsus
<i>L. griseus (hendersoni or griseus)</i>						
US 375746	??*	Recife, Brazil.....	2 Jan. '44	62.2	142	34.4
US 740888	♂?	Brazil.....	?	55.3	137	33.0
HBC 16476	♂	Colombia.....	17 Sept. '45	54.9	139	33.0
CM 64050	♂	Mangunca I., Brazil....	10 Mar. '24	54.2	138	33.4
CM 64051	♂	Mangunca I., Brazil....	19 Mar. '24	53.2	134	30.8
<i>L. scolopaceus</i>						
US 103365	♀	Guatemala.....	?	72.2	148	41.1
US 132227	♀	Guatemala.....	?	76.1	144	39.4

** Unsexed; probably a female.

eastern Canada and along the Atlantic coast; it winters chiefly in the eastern Caribbean area. *L. g. hendersoni* migrates through the Mississippi Valley and the Great Lakes region to both the Gulf and Atlantic coasts and thence southward over the whole of the Caribbean region to the northern and north-western coasts of South America. *L. g. caurinus* migrates along the Pacific coast southward as far as Ecuador and Peru. There is a considerable overlap in the winter ranges of *griseus* and *hendersoni*; between *hendersoni* and *caurinus* overlap also occurs, but apparently not so extensively.

The wintering range of the species as a whole may be summarized as follows: northward along the Atlantic coast to South Carolina (Bird Key, Long Island, Mount Pleasant, etc.), on the Gulf coasts (Rockport, Texas) and along the Pacific coast to Point Concepcion (Alamitos Bay, Los Angeles County; Point Mugu, Ventura County), less commonly farther north on Morro Bay, Monterey Bay, and San Francisco Bay (Dumbarton Bridge; Alviso); southward through the whole of the Caribbean area to the northern coast of South America as far east and south as Recife, Brazil, southward along the Pacific coast to Peru (Vegeta). All winter-taken specimens of *L. griseus* from California were obtained at salt- or brackish-water localities; so far as I can tell, this is true of the large majority, if not all, of other winter-taken specimens from all remaining parts of the known range.

Records of summer-taken, nonbreeding individuals of *L. griseus*, collected in various parts of the winter and migratory range, are listed in table 28. All June-taken specimens in breeding plumage are included; and some specimens taken in the first half of July in areas other than the Atlantic coast, where short-billed dowitchers appear in migration at that time (Stone, 1937: 480), are also included for reasons of distance from breeding grounds, or of association with collected specimens of obvious nonbreeders, or both.

The records summarized in table 28 total 115. They indicate that nonbreeding individuals may be expected throughout the entire range of *L. griseus*

TABLE 28
OCCURRENCES OF NONBREEDING INDIVIDUALS OF *LIMNODROMUS GRISEUS*

State, province, or country	Date	Plumage		
		Summer	Mixed	Winter
Ecuador.....	July 18-Aug. 3..... Aug. 18.....	1 ♀ *	1 ♀ *	3 ♂, *3 ♀ * 1 ♀ *
Baja California.....	June 13.....		1 ♀ *	1 ♂ *
Texas.....	June 11-July 9..... July 14-19.....	1 ♀, 1 ♂ *	2 ♂, *2 ♀ *	1 ♂ *
Louisiana.....	June 2-17.....			2 ♂, *1 ♀ *
Mississippi.....	July 11-24.....	1 ♂, 2 ♂ *	2 ♂, *2 ♀ *	
Alabama.....	July 5.....	1 ♂, *1 ♀ *		2 ♂ *
Florida.....	May 21-28..... June 6-July 8.....		3 ♀ *	3 ♀ * 2 ♂, *1 ♀ *
South Carolina.....	May 20..... June 7-8.....			1 ♂ * 2 ♀ *
North Carolina.....	July 5-11..... August 1-4.....		1 ♂, *3 ♀ *	1 ♂, *1 ♀ * 8 ♀ *
Virginia.....	June 2..... July 20.....	1 ♂ *	1 ♂ *	
Massachusetts.....	June 18.....		1 ♀ *	
New York.....	June 7.....	1 ♂ ?		
New Hampshire.....	June 21.....	1 ♂ *		
North Dakota.....	June 15-23.....	1 ♂, 1 ♀, 1 ♀ *	1 ♂, *2 ♀ *	
California.....	June 2-July 15..... May 16-27..... July 30.....	4 ♂, 3 ♂, * 4 ♀, 22 ♀ *	1 ♀, 3 ♀ * 1 ♀ *	1 ♂ * 2 ♂, *5 ♀ *
Total numbers of specimens.....		47	27	41

* First-year birds, many of them with juvenal rectrices. Retention of juvenal rectrices occurs most commonly among specimens showing evidence of partial prenuptial molt or no molt at all (mixed and winter plumages above). Specimens not marked with an asterisk are either adults or first-year birds.

where suitable habitat is found, and that these individuals undergo all degrees of the prenuptial molt or that this molt is omitted. In most of them it is evident that the postjuvenal molt was not so extensive as usual, a condition which makes possible the identification of the majority of these non-breeders as first-year birds. It would seem to indicate that the physiology

underlying abortive migratory behavior and prenuptial molt, or the absence thereof, manifests itself as early as the previous winter or late fall. Nonbreeding individuals which have not undergone a prenuptial molt pass through the first complete molt apparently at various times during the summer or early fall. *L. griseus* appears to differ significantly from *L. scolopaceus* (table 16) in the relative preponderance of individuals in mixed or winter plumage.

DISCUSSION OF GEOGRAPHIC VARIATION

In the foregoing sections it has been shown that two major variational trends exist in *L. griseus*: first, a trancontinental size cline, *L. g. caurinus* of Alaska being the large extreme, *L. g. griseus* of eastern Canada the small

TABLE 29
SEXUAL DIMORPHISM IN DIMENSIONAL CHARACTERS IN DIFFERENT POPULATIONS
OF *L. SCOLOPACEUS* AND *L. GRISEUS*
(Shown as per-cent difference between females [100 per cent] and males)

Species	Wing	Culmen	Tarsus
<i>L. scolopaceus</i>			
California.....	-3.6	-14.0	-7.9
Alaska.....	-3.4	-13.3	-7.0
<i>L. griseus</i>			
California.....	-1.9	-8.4	-2.8
Alaska.....	-2.7*	-8.5	-4.2*
Alberta.....	-1.6	-7.8	-3.2
Manitoba.....	-2.0	-7.5	-3.5
Eastern Canada.....	-1.1	-6.2	-1.7

* Excessively high estimates based on small sample of females.

extreme; and second, a trend in ventral plumage color from an extensively white, heavily spotted extreme in *L. g. griseus* to an extensively buff, only lightly or obsolescently spotted extreme in *L. g. hendersoni* of interior Canada. Both extremes of color occur in the exceptionally variable, westernmost population, *L. g. caurinus*. The geographic trend in size thus differs from that in color characters.

Practically no information is available on the environmental relations of the several races on their breeding grounds, and the significance of the observed variation remains unknown. At least we can say that, so far as size is concerned, no relation to the so-called ecological rules of Bergman and Allen (Huxley, 1942:212) is indicated. The largest of the races both breeds and winters along the Pacific coast, in areas having climates warmer than, or at least similar to, those inhabited by the smaller races in corresponding seasons to the east. But the observed differences in size do strongly suggest that between the populations at the extremes of the cline some marked difference or differences in environmental relations exist. Correlated with the cline in size is an eastward reduction in sexual dimorphism of mensural characters (table 29).

A specimen of great interest in the variational trends of *L. griseus* is a female of the nominate race collected at Marshfield, Massachusetts, on May 25, 1933, by J. L. Peters (MCZ 157852). A sketch of the ovary appears on the label, and this, together with plumage characters, indicates that the specimen is an adult. Wing and culmen measure 136 and 56.7 mm., respectively; but the tarsus measures only 24.6 mm. (see pl. 10). The mean tarsal length of females of *L. g. griseus* from the North Atlantic coast is 34.35 mm. (table 24), $\sigma = 1.37$, and $34.35 - 3\sigma = 30.24$. Thus, this individual falls astonishingly far below the expected range of population variability.

In shortness of tarsal length this specimen may be a developmental freak, or a mutant, or both, of course, and a few speculations concerning it are worth while. In the first place, if judged correctly to be an adult, at the very least this individual was approaching two years of age when collected. This would indicate that in life it was not seriously handicapped by its short legs. Secondly, this individual was derived from a population which in size already represents the small extreme in the species as a whole, and it thus suggests the possibility of further tendency toward reduction in size.

THE PROBLEM OF SPECIES DISTINCTION

The evidence presented in the foregoing sections demonstrates a series of fundamental differences between *L. scolopaceus* and *L. griseus*. These concern color tone and color pattern in all plumages, size, ratio of body parts, sexual dimorphism, extent of molt, length of molt period, ecological distribution, geographical distribution, and period of migration. Brooks (in Brooks and Swarth, 1925:128; and in Brooks, 1934:23) has stated that in migration the two kinds of dowitchers occur in separate flocks. Urner (1935:465) and Peterson (1947:262) have described differences in call notes. Further studies of all aspects of behavior of the two kinds of dowitchers should be made.

In other words, the only really good basis at present for a discussion of the relationships of *scolopaceus* and *griseus* is data on distributional and morphological differences. The discussion cannot be conclusive, these differences notwithstanding, for the reason that their ranges are allopatric and that nothing is known of the behavior and local distribution of these forms in regions where they may meet. Reasons for considering them as species may now be discussed.

EVIDENCE FROM DISTRIBUTION

The long-billed dowitcher, apparently throughout its range, is a bird chiefly of fresh-water ponds and lagoons. Its preference for this habitat in California has been demonstrated. Information from other parts of the Pacific coast presents essentially the same picture, as does that from other areas from which adequate specimen records are available. In Florida, for example, at least 75 per cent of the records of *scolopaceus* were obtained at interior, fresh-water localities, whereas all the records of *griseus* were obtained at coastal localities.

It is likely that a certain number of records of *scolopaceus* from coastal localities actually were taken on more or less permanent, still, fresh-water

lagoons at various short distances from the coast. Such situations are to be found in southern Texas, northeast of Brownsville, for example, where a flock of 15 winter-plumaged dowitchers was observed on a lagoon not far from the coast in June, 1937 (Pitelka, 1938). Marine shores and coastal inlets with some tidal flow are also available to dowitchers on the Texas coast, and since both species occur there, some habitat segregation may be expected.

On its breeding grounds, in the Hooper Bay region, Brandt (1943:387) reports *scolopaceus* as "confining itself almost entirely to the moist upland

TABLE 30
REGIONAL DIFFERENCES IN RELATIVE OCCURRENCE OF *L. SCOLOPACEUS* AND *L. GRISEUS*
IN INTERIOR NORTH AMERICA

Region	<i>L. scolopaceus</i>		<i>L. griseus</i>		Total
	Number of specimens	Per cent	Number of specimens	Per cent	
Rocky Mountains, Great Basin, interior Mexico south to Jalisco.....	71	97.3	2	2.7	73
Mississippi Valley (North Dakota and Wisconsin south to Texas and Mississippi)*....	97	44.7	120	55.3	217
Great Lakes region.....	14	23.7	45	76.3	59

* Records from the Gulf coast of Texas, Louisiana, and Mississippi are included.

fresh-water meadows." He states also (p. 212) that "its peculiar, sedgy, muskeg sort of nesting habitat in our area was limited, yet it fed far and near..." and (p. 214) that the long-bill fed along "shallow, reed-fringed pond shores of the tundra, often at a distance from its home." These are the most definite statements concerning habitat relations of *scolopaceus* on its breeding range which I have been able to find. Brief mention of habitat in most other sources more or less corroborates them. But that dowitchers occur in salt- or brackish-water habitats in Alaska at least during the postbreeding period of dispersal and as migration is undertaken is indicated by Nelson's (1887:101) report of their presence on muddy flats and tidal creeks in early September. No information on habitat relations of dowitchers along the Arctic coast is available, but a general description of the tundra environment where they occur is given by Johansen (1924:9).

Whereas the short-billed dowitcher is so evidently a denizen of salt- or brackish-water habitats on its wintering grounds and also on its migratory routes along both coasts, it occurs in fresh-water habitat along interior migratory routes and on breeding grounds in Canada and Alaska. The main areas of occurrence in the interior of North America are the Mississippi Valley and the Great Lakes region, through which areas *griseus* moves more or less directly to the Gulf and Atlantic coasts. Specimen records for the interior of the continent, south of the Canadian border, summarized in table 30, bear

this out. Thus, relative to *scolopaceus*, *griseus* is uncommon to rare in the Rocky Mountain and Great Basin areas and the interior of Mexico; but it increases markedly in abundance in the Mississippi Valley and in the Great Lakes region. This is in agreement with Swenk's (1940:71) finding that his records of short-billed dowitchers for Nebraska were limited to the eastern part of the state, whereas the long-bill was recorded from all parts of Nebraska.

The characteristic breeding habitat of *griseus* in interior Canada is muskegs, that is, low marsh or bog vegetation often surrounding small glacial lakes and ponds (Bent, 1927:109; Rowan, 1927:217). Muskegs typically occupy areas of varying size between patches of forest and are themselves frequently dotted with tamaracks and black spruces. Such habitat is occupied not only in Alberta and undoubtedly other parts of the interior Canadian range, but also at Churchill on Hudson Bay (Taverner and Sutton, 1934:8-9, 46). Although at the latter locality dowitchers have access to tidal flats, they are not reported to occur on them in numbers until early August, after at least local migratory movements have begun. Speaking of muskeg areas in Alberta where both dowitchers and greater yellow-legs (*Totanus melanoleucus*) breed, Rowan (1929:17) states: "Many of the muskeg lakes are certainly no good whatever to a Shank [yellow-legs] as feeding-grounds, for they have no muddy shores, the floating vegetation overlapping the margins far beyond the solid limits underneath. The birds might therefore well have to travel a few miles for food." The same point may apply to dowitchers.

In the vicinity of Yakutat, Alaska, Shortt (1939:15) reports that dowitchers, herein shown to represent *L. griseus*, breed in muskegs along the Situk River. In the Bristol Bay region at the base of the Alaska Peninsula, Hurley (1931:7, 1932:17) found dowitchers breeding on the tundra, among marshes and pools close to a river with tidal flow. Here the tundra is dotted with islets of alders, willows, and small spruces, and is thus more or less comparable ecologically to that of interior Canadian areas.

According to both Rowan and Hurley (*loc. cit.*), the nest is in or at the base of a hummock on relatively dry or moderately wet sites in wet, grassy meadows. Information on nesting sites of *L. scolopaceus* (see, for example, Conover, 1926:305; Brandt, 1943:387) does not indicate that it differs from *L. griseus* in any significant way.

The foregoing represents substantially all the significant evidence on breeding habitat of the two species now available. We do not know how they utilize the borders of inland, fresh-water areas for needs of feeding, loafing, and shelter, how much these relations differ in areas where breeding dowitchers have access to tidal flats, or what the spatial relations of breeding pairs are. The limited evidence now available does not reveal any significant differences in habitat relations, but that evidence is so scanty as to be virtually worthless. Certainly the morphological differences between *scolopaceus* and *griseus* and the trancontinental size cline for *griseus* indicate that some real differences occur. Certainly also the observed mensural differences are of adaptive significance, at least in areas of wintering and migratory occurrence (see further on).

Distributional facts presented in this and earlier sections permit the following conclusions: The general breeding habitat of *scolopaceus* is the tundra of northern and western Alaska; that of *griseus*, on the basis of both known and presumed breeding areas, is the more northern part of the transcontinental boreal forest, that is, the broad zone of more or less stunted tree growth intermixed with extensive muskegs and tundra, from the Ungava Peninsula to southern Alaska.² Both species use grassy marsh areas for nesting and feed along pond and lake margins often at considerable distances from nesting sites. There are no records of *L. griseus* north of the tree limit in the breeding season. In migration *scolopaceus* occurs from the Pacific coast throughout the interior to the Atlantic coast, becoming increasingly rare eastward. *Scolopaceus* is a bird of fresh-water ponds and lagoons. *Griseus*, on the other hand, is abundant on both coasts and in the interior only in the Mississippi Valley and the Great Lakes region. At least along the Pacific and Atlantic coasts and on its wintering range, *griseus* is a bird of coastal mud flats and inlets with tidal flow. Northward limits of winter distribution are approximately the same for *griseus* and *scolopaceus*, but southward limits differ markedly: *scolopaceus* is not known to winter south of Guatemala, whereas *griseus* is widely distributed south to Brazil and Peru and throughout the whole of the Caribbean area.

EVIDENCE FROM MORPHOLOGY AND ADAPTIVE MODIFICATIONS

The morphological evidence provides at least three arguments for the view that *griseus* and *scolopaceus* represent distinct species: First, not only do bill, wing, and tarsus differ in average size, but the differences are of opposing sign. Whereas bill and tarsus are longer in *scolopaceus* than in *griseus*, the wing is shorter. These differences are apparently correlated with dissimilarities in habitat and feeding behavior.

L. scolopaceus has been shown to inhabit chiefly fresh-water areas, and its longer bill and longer tarsi evidently represent adaptations whereby the area of water-covered pond margin that can be explored effectively for food is increased. The long-billed dowitcher, and for the most part the short-billed dowitcher also, wades when feeding, probing the soft bottom for various invertebrates or seeds and often immersing the head partly or entirely (see Grinnell and Hunt, 1929:68; Stone, 1937:481; and Sperry, 1940:19). In fresh-water habitats, the long-bill feeds without benefit of the tidal fluctuations that increase the foraging area for the short-bill. The short-billed dowitcher feeds occasionally on recently exposed flats and usually in shallow water, at the margin of the receding tide or in pools left by the tide. For types of food taken by dowitchers see Preble and McAtee (1923) and Sperry (1940).

The difference between *griseus* and *scolopaceus* in wing size opposing that of bill and tarsus may well be a part of the complex of adaptational modifi-

² The apparent confinement of *L. griseus* to areas within tree limit is of interest in conjunction with the fact, first, that it is evidently a member of the boreal fauna forced southward by glaciation, and second, that records of Pleistocene vegetation in the northern United States do not indicate a tundra zone between ice limits and forest (Rosendahl, 1948; Sears, 1948).

cations in *scolopaceus*. Were the wing of that form of a size proportional to tarsus as in *griseus*, its average length in females would be 165 mm. rather than 146 (calculated from data in tables 7 and 8). A wing of this size would probably hit the surface were the bird standing in one or two inches of water, and the success of the take-off would thus be more or less impaired. The two dowitchers have not been studied for possible differences in beat of flight or in manner of flight take-off, but in two so closely related forms it is unlikely that any occurs. *Scolopaceus* evidently feeds in water of greater average depth than *griseus*; and under these circumstances the reduced wing length would permit in general a flight take-off more effective, through greater speed and better control, than it would be if the wing were much longer.

Thus, differences between *scolopaceus* and *griseus* in wing as well as in bill and tarsus are considered to represent adaptive modifications whereby *scolopaceus* as a species better exploits fresh-water habitats. By itself, the fact of these adaptive modifications is not an argument for the specific distinctness of *scolopaceus*; yet the observed differences do seem to be more marked than those between races of most other well-studied species.

A second argument for the specific distinctness of *scolopaceus* is afforded by the marked difference between that form and *griseus* in sexual dimorphism of mensural characters. Sex for sex, there appears to be no real difference in variability of *scolopaceus* and *griseus* (tables 7 and 8); but greater disparity in size between males and females of *scolopaceus* means greater variability in total population. This again seems to be significant in the adaptive trend displayed by that form.

It has already been pointed out that increased length of bill and tarsus and decreased length of wing permit *scolopaceus* to feed in water of greater average depth than *griseus*, and thus to increase the breadth of its total forage zone along the periphery of a shallow pond. This advantage, if we may call it that, is augmented by the greater difference in sexual dimorphism in *scolopaceus*. Intersexual differences in feeding habits are unlikely, but the statistical consequence of the greater disparity in size between males and females of that species is, again, to increase the total forage area which the species can use successfully. The difference in sexual dimorphism between *scolopaceus* and *griseus* seems to me to indicate, more than any other single fact, that we are dealing with two genetic systems which have become differentiated beyond the racial level.

A third argument for the specific distinctness of *scolopaceus* is the absence of undoubted intermediates or hybrids between that form and *griseus* in the extensive collections examined in this study. In the first place, difficulty in distinguishing certain individual specimens in winter plumage by characters of that plumage is not an argument that these represent intermediates. As pointed out earlier (p. 10), winter plumages of the dowitchers are closely similar, as is observable in other species pairs or species groups among charadriiforms.

Still another spurious source of evidence for intermediacy of certain specimens is the juvenal plumage in *L. g. caurinus*, geographically closest to

scolopaceus. In *caurinus* only among the races of *L. griseus* there is some darkening (increased reddishness) of the buff edgings of dorsal feathers, and this, with reduction in extent of subterminal marks on scapulars (see, for example, MCZ 234010, ♀, Izembek Bay; US 58730, ♂, Fort Kenai), results in a dorsal coloration darker, at least in some summer-taken juveniles from Alaska, than is found in *L. g. hendersoni* or *L. g. griseus*. These individuals thus suggest *scolopaceus*; but their dark coloration does not necessarily indicate that *L. g. caurinus* interbreeds with *scolopaceus*, since under conditions of humid maritime climate prevailing in coastal Alaska the tendency toward dark dorsal coloration observed in *caurinus* is not unexpected.

A puzzling specimen is a juvenile (US 81255) collected on August 30, 1879, at St. Michael, Alaska, by E. W. Nelson. A ventral wash of light rust and a noticeable amount of brown on the crown suggest *griseus*; however, the rest of the dorsal plumage and the tail feathers display the characters of *scolopaceus*. It is marked "♀" and its dimensions are: wing 145 mm., culmen 60.6, tarsus 36.9. If the specimen was correctly sexed, then its dimensions would be those of *L. griseus*. However, it was collected in the range of *scolopaceus*, at the same time and place as two other juveniles (ROM 26088, 26089) that clearly represent *scolopaceus*. These facts, together with the absence of undoubted specimens of *griseus* from localities north of the Bristol Bay region, cause me to consider Nelson's specimen a missexed individual of *scolopaceus*. I do not deny that the color characters suggesting *griseus* in that specimen could be regarded as evidence of at least sporadic genic interchange between *scolopaceus* and *griseus*, but what seems more likely to me at present is that they merely represent extremes in the variability of *scolopaceus*.

Among adults, there are four or five Pacific coast specimens with ventral spotting concentrated on the breast, the resulting pattern suggesting *scolopaceus*, for example, KR 556 and 557, both from Tofino, B.C. (see pl. 4). Unlike typical *scolopaceus*, these specimens, which are extremes for this character, bear scattered obsolete spots on the lower breast and belly, as is true of the others that display the same character of spot concentration to a lesser degree, for example, CM 133756, from Motordrome, California. The dimensions (in mm.) of these specimens, given below, are clearly those of *L. griseus*.

	KR 556, ♀	KR 557, ♀	CM 133756, ♂
Wing	149	149	147
Culmen	63.4	60.5	62.1
Tarsus	37.6	38.9	37.2

Thus, the few specimens that superficially suggest intermediates between *griseus* and *scolopaceus* prove, upon closer examination, to do so only in one or two characters, whereas in others they are representative of one or the other form. Considering the fact that no adult and but one juvenal specimen of *scolopaceus* suggesting intermediacy was found, the specimens of *griseus* just described are best regarded as extremes in the wide variation of color characters already demonstrated in *L. g. caurinus*. It may be recalled that ventral ground color in *L. g. caurinus* is at times as intense and as extensive

as in *L. scolopaceus*, and that in these specimens ventral spotting is reduced or obsolete. All these facts considered together suggest that *caurinus*, closest to *scolopaceus* geographically, may be expected to resemble a segment of the presumably continuous, freely interbreeding populations which once connected parent populations of *scolopaceus* and *griseus* (see further on). If this point is valid, then the occasional emergence of *scolopaceus* characters in *L. g. caurinus* is not surprising.

In other words, not a single convincing instance of intermediacy between *griseus* and *scolopaceus* has been found among specimens examined in this study. It is true that overlap in characters is such that an occasional hybrid specimen may be lost, but, as has already been pointed out in the analysis of Californian populations, were there any significant amount of interbreeding between *griseus* and *scolopaceus*, some evidence of it would almost certainly be detected. Actually, the arrays of specimens segregated according to plumage characters displayed normal curves of variability, overlap of unit characters notwithstanding.

These results, it may be argued, do not exclude the possibility of sporadic interbreeding, and, as has already been pointed out, critical areas where evidence of such interbreeding may be sought remain to be explored. The genetic behavior of characters in actual crosses of *scolopaceus* and *griseus* may not necessarily lead to the quantitatively intermediate expressions that we seek for evidence of interbreeding. Instances of interbreeding might thus be obscured. While this could be true of plumage characters, it is probably not so of mensural characters, and specimens discussed above suggesting intermediacy in certain plumage characters did not do so in mensural characters.

The sum of evidence on distribution, morphological variation, sexual dimorphism, the presumed significance of morphological differences, and supposed intermediates between *griseus* and *scolopaceus* indicates, therefore, that morphological discontinuity between them, if not complete, is almost so. Conclusive proof on the relations of these forms must be sought in southwestern Alaska between Cape Constantine and Point Dall and in northwestern Mackenzie.

HISTORICAL INTERPRETATIONS

Rand (1948), drawing upon the botanical investigations chiefly of Hulten (1937) and Raup (1946), has recently provided an interpretation of the distributional patterns and correlated evidence of species formation in a number of North American birds which breed in the Arctic. The arguments arising from these studies are briefly as follows: It is recognized that geographic isolation is evidently a necessary prelude to species formation. Since among Arctic American species or species groups exemplifying steps in that process a number have passed beyond the subspecies level, it is held that an isolating factor, Pleistocene glaciation, has separated previously connected populations into disjunct units which have undergone evolutionary change. On the reestablishment of contact, these units have reacted variously. That this event was, in a geological sense, a relatively recent one in the history of these popu-

lations which react or appear to react as species, is indicated by the fact that either their ranges are allopatric or there are only small areas of sympatry. Refugia, or nonglaciaded areas (Flint, 1947), figure importantly in this history, and one in particular, the Bering Sea-Yukon refugium in Alaska, bears upon the facts derived from this study of dowitchers.

Among the "semi-species" in the Arctic American avifauna discussed by Rand, the histories of two are evidently more or less parallel to that of *Limnodromus*: *Gavia immer* and *G. adamsi* (loons), and *Parus hudsonicus* and *P. cinctus* (chickadees). In each of these pairs, it appears that the first moved south as Pleistocene glaciation reached its maximum, whereas the second was confined to the Bering Sea refugium. (For a general discussion of speciational dynamics under such conditions as are described here, and for a record of observed effects of Pleistocene glaciation in Europe, see Mayr, 1942:263-265.)

The present-day breeding range of *L. scolopaceus* agrees rather remarkably with the coastal Alaskan part of the Bering Sea-Yukon refugium, and the few known records from northeastern Siberia, also a part of that refugium, indicate further agreement. It is conceivable that the present-day restriction of *scolopaceus* to fresh-water habitats may have been effected through confinement to that northern refugium when, at the time of glaciation, upland fresh-water ponds were the chief feeding sites available to shore birds.

The transcontinental range of *L. griseus*, on the other hand, typifies species which occurred well to the south at the time of maximal glaciation. Recent geographic variation is at least in part related to the isolation afforded by two barriers: the Rocky Mountains of western Canada extending northward into Alaska, which, so far as known now, completely isolate *caurinus* from *hendersoni*; and the Hudson and James bays, which partly isolate *hendersoni* from *L. g. griseus*. It may be suggested that as the biota of the tundra and boreal forests followed the receding glaciers, division of the range of *L. griseus* into Pacific coast, interior, and eastern sections has at least served to maintain, if not to accelerate, the trends of differentiation which that species displays. The western North American mountains which now isolate *caurinus* from *hendersoni* probably did so, too, throughout the Pleistocene and earlier, and in the earlier period *L. griseus* of the Pacific coast may have been restricted to southern Alaska and sections of the coast south to Puget Sound (see Hulten, 1937:41). In other words, there is good reason to believe that the differentiation seen in *L. griseus* antedates the time of the maximum of Pleistocene glaciation and may even be pre-Pleistocene in origin.

This suggestion does not necessarily do violence to the earlier one that the restriction of *scolopaceus* to fresh-water habitats may be of Pleistocene origin. Some geographic variation within the superspecies of American dowitchers may have existed in pre-Pleistocene times; and if so, the present-day transcontinental cline in *L. griseus* may have developed therefrom. The modifications observed in *scolopaceus*, more marked than any interracial differences in *griseus*, but associated as they are with different habitat relations, represent a shift to an adaptive peak (Simpson, 1944:206-208) unlike that of *L. griseus* and could have begun to take place no farther back than the middle or early Pleistocene.

SUMMARY AND CONCLUSIONS

Evolutionary trends in the American shore-bird genus *Limnodromus* were examined through a study of distribution and geographic variation based on 2,908 specimens. Two closely similar, migratory species of "waders," characteristic of pond margins and tidal flats, comprise that genus: *L. scolopaceus*, which is relatively long-billed, long-legged, and short-winged, and *L. griseus*, which is relatively short-billed, short-legged, and long-winged.

L. scolopaceus breeds in northern and western Alaska; it migrates along the Pacific coast, through interior Canada, and over the whole of the United States, becoming less common eastward. *L. griseus* breeds in southern Alaska, interior Canada, and probably Ungava; as a migrant it is abundant on both coasts, but it occurs commonly in the interior only in the Mississippi Valley and the Great Lakes region. Northward limits of winter distribution, in the southern United States, are approximately the same in *griseus* and *scolopaceus*; but southwardly *scolopaceus* does not occur beyond Guatemala, whereas *griseus* is widely distributed southward to Peru and Brazil.

L. scolopaceus, previously considered not to differ significantly from *L. griseus* in habitat relations, is shown to prefer fresh-water ponds and lagoons in most and probably all parts of its range. On the other hand, *L. griseus*, at least along the Pacific and Atlantic coasts and on its wintering range, is a species frequenting coastal mud flats and inlets with tidal flow; but it occurs in fresh-water habitats on its breeding range and along interior migratory routes. In California, salt-water occurrences of *scolopaceus* are chiefly those of migrants and first-year birds; fresh-water occurrences of *griseus* are chiefly those of spring migrants. Along the Pacific coast, fall migration occurs earlier in *griseus* than in *scolopaceus*; the time of spring migration is the same.

Two levels of divergence are evident in the genus *Limnodromus*: a primary one between long-billed and short-billed forms, and a secondary one expressing itself as a transcontinental cline in *L. griseus*. *L. scolopaceus* differs from *L. griseus* in color tone and color pattern in all plumages, in size, in ratios of body parts, in sexual dimorphism of mensural characters, in extent and rate of postjuvenal molt, in prenuptial molt, and in ecological distribution, geographical distribution, and period of fall migration. Some of these differences, though minor, are nevertheless real. No undoubted morphological intermediates between *griseus* and *scolopaceus* were found. Morphological discontinuity between them, if not complete, is almost so, and they are accorded specific rank even though their breeding ranges are allopatric.

Two geographic trends of variation occur in *L. griseus*: a transcontinental size cline, the large extreme occurring in Alaska, the small in eastern Canada; and a variation in ventral color from a heavily spotted, extensively white extreme in eastern Canada to a sparsely spotted, extensively buff extreme in interior Canada. Both of the latter extremes occur in the Alaskan population. On these bases, three races may be recognized: *L. g. griseus* of eastern Canada, *L. g. hendersoni* of the interior and *L. g. caurinus* of Alaska, the last newly described in this paper. Extensive series of specimens from the Atlantic coast

show that *L. g. hendersoni* occurs there commonly as a migrant from Chesapeake Bay southward as well as on the Gulf of Mexico.

L. scolopaceus is considered to have been derived from a form similar to *L. griseus*. The long bill, long tarsus, short wing, and marked sexual dimorphism in size of *scolopaceus* are regarded as modifications whereby that species has become better adapted to its fresh-water habitat. It is suggested that at the time of the maximum of Pleistocene glaciation *L. scolopaceus* was confined to the Bering Sea-Yukon refugium, with which its present-day breeding range agrees closely, whereas *L. griseus* occurred to the south of glaciated areas. Restriction of *scolopaceus* to fresh-water habitat and correlated morphological modifications are considered to have resulted in part at least from its restriction to inland breeding areas in the period of glaciation. Racial differentiation within *L. griseus* as a whole is believed to antedate the time of maximal Pleistocene glaciation.

Close examination of the sequence of molts and plumages in *Limnodromus* has provided criteria for segregation of first-year and adult birds vital to analyses of variation. The data include observations on molt previously unrecorded or at variance with earlier work. Results of a critical survey of the literature on taxonomy and nomenclature in the genus *Limnodromus* are summarized in an appendix.

APPENDIX

TAXONOMY AND NOMENCLATURE

The objectives of this appendix are several: first, to place on record the results of a survey of the literature dealing with the taxonomy and nomenclature of the dowitchers; second, to provide synonymies of the recognizable forms which embody the results of that survey; and third, to supply a list of specimens examined.

The literature on dowitchers, especially that dealing with the western half of the North American continent, is an almost inextricable confusion of records. Ridgway's (1919:202-204) synonymy for *Limnodromus griseus scolopaceus*, for example, consists of records which apply to *L. scolopaceus*, or to either or both western races of *L. griseus*, or to all three. As Brooks (1934:23) remarked, "The practice of calling all western birds *scolopaceus* has perpetuated a mass of error." The situation is not much less confused in the East. The fact that *L. g. hendersoni* occurs regularly along the Atlantic coast has been recognized only recently. A number of records of *L. g. griseus* apply to this race, as do also some east coast records of *L. scolopaceus* since certain observers from the 1850's to the 1930's considered specimens with buffy, sparsely spotted under parts to represent the "western race," apparently whether they were long-billed or not. These circumstances have made it necessary for me to disregard all published records which are not supported by usable data on plumage or mensural characters or which are not confirmed by specimens which I have examined.

A partial review of the dowitcher problem has been published by Swenk (1940), and little is to be gained by a detailed résumé of its early history. Accordingly, only significant recent statements concerning taxonomy and distribution will be summarized here. Essentials of the nomenclatural histories of the recognizable forms prior to the publication of the latest edition of the Check-list of North American Birds (American Ornithologists' Union, 1931), so far as these can be correctly ascertained, are recorded in the synonymies provided further on.

The A.O.U. Check-list (1931) divides the species *Limnodromus griseus* into eastern and western races, *L. g. griseus* and *L. g. scolopaceus*, respectively. In the following year, Rowan described an inland population, *L. g. hendersoni*, characterized by larger size, reduced ventral spotting, and more extensive buffiness ventrally in comparison with the nominate race in eastern Canada. He also held that *scolopaceus* was specifically distinct. Peters (1934), in his "Check-list of Birds of the World," did not consider *hendersoni* recognizable, and his treatment of the dowitchers agrees with that of the A.O.U. Check-list in all essentials.

Since 1932, the distinctness of the inland race *hendersoni* has been upheld by Brooks (1934), Swenk (1940), Conover (1941), van Rossem (1945), and Aldrich (1948). Most other students of the dowitchers have recognized only the two races defined by the A.O.U. Check-list and by Peters (*loc. cit.*).

At the time Rowan introduced the question of a recognizable inland race, the occurrence of a short-billed form of the dowitcher on the Pacific coast was already under study. Increasing awareness of this fact is evidenced by a series of papers appearing in the period 1925-1940 (Brooks and Swarth, 1925; Bent, 1927; Taverner, 1928; Rowan, 1932; Brodkorb, 1933; Willett, 1933). Brooks (1934:23) maintained, and for the first time openly, that short-billed dowitchers occur commonly on the Pacific coast. Orr (1940:63) concluded that the "eastern" or short-billed form "*griseus* outnumbers [the long-billed form] *scolopaceus* in California by about 5 to 1," thus upsetting the concepts of regional representation of races held at least as recently as 1934.

Whatever the relative representation of the two forms, the papers just cited established that both long-billed and short-billed dowitchers occur commonly on the Pacific coast. But as this fact has emerged, opinion has differed with respect to whether the short-billed dowitchers of the Pacific coast represented *hendersoni* (Rowan, 1932; Brooks, 1934; Taverner, 1935), or *griseus*, including *hendersoni* (Brodkorb, 1933; Willett, 1933; Orr, 1940), or both *hendersoni* and *griseus*, the latter represented by vagrants (Conover, 1941; Aldrich, 1948). That the breeding range of the short-billed dowitcher east of Hudson Bay remains unknown has led some taxonomists (for example, Brodkorb and Orr) to question the validity of the inland race, *hendersoni*. Rowan (1932) and others have argued that the characters displayed by eastern Canadian specimens are not those of the inland populations, and that, although the breeding grounds of the eastern form are not known, the distinctions made between that form and *hendersoni* are geographically significant and valid. Recently, Aldrich (1948) has reported the "discovery" of a specimen in breeding plumage collected at Fort Chimo, Quebec, on June 10, 1883, deposited in the collections of the United States National Museum. This specimen, US 94471, was collected and reported by Turner (1885:246); reference to the record is made by Ridgway (1919:199), Bent (1927:109) and Austin (1932:10). The characters of this supposedly breeding specimen are those attributed to the nominate race by Rowan and Conover, whose views are thereby supported.

Finally, throughout the time that the foregoing questions have been under study the specific distinctness of *scolopaceus* has been questioned; only Rowan (1932), Brooks (1934), Conover (1941), and van Rossem (1945) among recent authors have held to the opinion that *scolopaceus* is distinct.

Thus, several more or less discrete problems are presented by the dowitchers, and simultaneous study of various of them over the last fifty years, with the use of limited material, has as often confused as clarified the answer to any one of them. It is worth while to enumerate these problems in summary: first, the existence of a western form, *scolopaceus*, distinct from *griseus*; second, the specific distinctness of *scolopaceus*; third, the existence of an inland form, *hendersoni*, distinct from *griseus* and *scolopaceus*; fourth, the occurrence on the Atlantic coast of both *scolopaceus* and a ventrally buffy, light-spotted dowitcher larger than typical *griseus*, later found to be *hender-*

soni and confused by many with *scolopaceus*; fifth, the lack of conclusive information concerning the breeding grounds of dowitchers east of Hudson Bay; sixth, the occurrence of short-billed dowitchers on the Pacific coast; and seventh, the racial status of the latter. So far as the data and statements available in the literature are concerned, only the first and sixth problems are considered to be settled conclusively.

Additional information of historical and nomenclatural importance or references thereto are given in the synonymies which follow. No effort has been made to include all references which can be allocated to one of the four forms with reasonable certainty; thus, various records carefully reported and in my opinion nomenclaturally correct have been omitted. But the number of such records is not large. In other words, a good part of what has been written about the distribution of dowitchers since the 1850's is virtually useless; and in most parts of southern Canada, the United States, the West Indies, and Mexico where dowitchers occur, because both species are present, their local occurrence and seasonal movements must be restudied.

The following types of citations have been entered into the synonymies: first, all names and combinations of names when used for the first time; second, all identifiable reports that are either critical to the distributional and nomenclatural record of a given form or recorded in the literature under an erroneous or incomplete name; third, a few important references to papers published before 1919 when Ridgway's monograph appeared; and fourth, all significant references subsequent to 1919. Citations not certainly identified with respect to the form to which they apply, but important to the nomenclatural record, are included; they are queried and appear but once in the synonymy of either *L. scolopaceus* or *L. griseus*. Whenever possible, locality records upon which a citation is based are given. Occasionally, when an author's use of a name or his records are only partly confirmed, that is, when no substantiating specimens have been examined, localities representing problematical records are queried. Published specific locality records confirmed by specimens examined in this study are followed by an asterisk. Sometimes, the original specimens used by a previous author have been examined in this study; and where it has proved possible thus to establish specific locality records, the records cited are followed by two asterisks.

Limnodromus scolopaceus (Say)

Limosa scolopacea Say, in James, 1823:170, original description. Type not extant, collected "near the Bowyer Creek" (Boyer River) near Council Bluffs, Pottawattamie County, Ia. According to Say's description, the type is a specimen in winter plumage, as pointed out by Orr (1940:62). Therefore, Brodtkorb's (1933:123) examination of it in terms of characters of the spring plumage is largely irrelevant. Datum of culmen length, $2\frac{3}{4}$ inches, indicates that Say probably had a female of *scolopaceus*, as has been pointed out by previous investigators. Say also states (*loc. cit.*), "tail, white, fasciate with black, which latter colour is more abundant . . ." This latter detail indicates another character of *scolopaceus*.

Scolopax longirostris Bell, 1852:3. Type, here designated, a female, collected by J. Bell on Long Island, N.Y., prior to 1852; deposited in the Academy of Natural Sciences of Philadelphia; see Lawrence (1852:4-5), who also figures this specimen (his pl. 1).

Bell's name, according to Lawrence (*loc. cit.*), is based on at least two specimens: a female in winter plumage representing *L. scolopaceus*, and a male in summer plumage, the latter also figured by Lawrence (1852:pl. 1), which appears to represent *L. g. hendersoni*. The name *longirostris* could thus be considered a composite one, and Lawrence's plate could be used as a basis for a shift of that name to the form now known as *hendersoni*. It is desirable to record available data on this matter in detail to insure that *longirostris* will continue to reside in the synonymy of *scolopaceus*. The case serves to point up some of the problems associated with identification of figured specimens when closely similar forms are involved.

One or both of the specimens discussed above may still be extant, but I have not been successful in locating and identifying them. Lawrence's plate may therefore serve as basis for selection of a type, and this has been done above. Bell's formal description of "*Scolopax longirostris*" is indefinite and applies to either *L. griseus* or *L. scolopaceus*. Selection of a type seems desirable, even though Bell clearly intended to do no more than provide a new name for Say's *Limosa scolopacea*, which Bell regarded as a valid form.

The female figured by Lawrence is thought to represent true *scolopaceus* for the following reasons: The rust color confined to the margins of the scapulars, the gray (not buffy) wash on the breast, and the reduced barring on the flanks are the characters of the winter plumage of that species, the margining of the scapulars indicating a first-year bird. The specimen was used by Bell in preparing his paper. Neither Bell nor Lawrence gives any dimensions from this specimen, but Lawrence comments that "it exceeds in size most of the individuals examined, which was the cause of Mr. Bell's attention being first called to it." Also, Bell's (1852:1) comment that he was able "to confirm the truth of Mr. Say's determination" indicates that he apparently had a specimen similar in color and size to the one described by Say (1823).

The male figured by Lawrence, originally in the collection of G. N. Lawrence, may represent *L. g. hendersoni*, "an adult in summer [with] entire lower parts uniformly rufous, the sides barred with black" (Bell, 1852:3). This specimen was an "exception" among those available to Bell, all others agreeing with Say's description of a bird in winter plumage. The text clearly agrees with the plate so far as plumage characters are concerned.

The Lawrence Collection, now in the American Museum of Natural History, contains no specimens of *L. g. hendersoni* which could be considered to be the basis for the figure of the male, but it does include an unsexed, first-year specimen (AM 45606) of *L. scolopaceus*, without date or locality, which represents an extreme variant of that form and which conceivably could have been the model for the male figured by Lawrence. Its dimensions are: culmen 72.4 mm., tarsus 41.4 mm., and wing (worn) 136 mm., and it thus represents a female (see table 6). Buffness of under parts and patterning of upper wing coverts and scapulars of the nuptial plumage agree with Lawrence's plate. This is also true of the buff bars of the tail, which are exceptionally wide for a specimen of *L. scolopaceus*, and of the whiteness of the chin, which is a character of first-year birds. Lawrence writes of a specimen with "lower parts

uniformly rufous," but the breast of this specimen is lightly and sparsely spotted. In this respect, it represents an extreme among first-year birds of *scolopaceus*, whose ventral spotting tends to be lighter and more dispersed than that of adults.

The Lawrence Collection contains another unsexed specimen of *L. scolopaceus* (AM 45605), without date but collected on Long Island, which also represents a first-year individual. On the basis of its dimensions, 45605 could be either male or female. It is not so extreme a variant, in the sum of characters enumerated above, as 45606. Moreover, its upper wing coverts are those of the winter plumage, a fact which eliminates it as a possible model for the figured male. In any case, both specimens could not have been available to Lawrence when his drawing was prepared, since he referred to his specimen in summer plumage as an exception among those he studied.

Thus, the identity of the figured male, using the evidence of the plate alone, is *L. g. hendersoni*; but with the knowledge that Lawrence might have had and used the specimen of *scolopaceus* described above, and assuming that he ignored or overlooked the obscure breast spotting, the figured male could represent an extreme variant of *L. scolopaceus*. I assume also that sex of the model specimen was not determined or known. In fact, the bills of the two figured specimens supposedly representing the two sexes are of identical length, even though in text Lawrence (1852:5) states that "the female exceeds the male in size . . ."

Macrorhamphus scolopaceus, Lawrence, 1852:45. Long Island, N.Y. See comments above.

[?] *Scolopax noveboracensis*, Heerman, 1859:66. California. Observed "in flocks on marshy ground and in the vicinity of ponds" [apparently referring to fresh-water sites, as is indicated by mention of specific localities under other shore-bird species]. It is likely that Heerman was concerned mainly if not entirely with *scolopaceus*.

Macrorhamphus griseus, Salvin and Selater, 1860:277. San Geronimo, Guatemala.

Macrorhamphus scolopaceus, Blakiston, 1863:131. Fort Carlton, Sask.

Macrorhamphus scolopaceus, Coues, 1866:271. Fresh-water ponds and lagoons, 2 or 3 miles inland from San Pedro Bay, Calif.

[?] *Macrorhamphus griseus*, Taczanowski, 1873:112. "In den nördlichen Gegenden Ost-Sibiriens, nämlich nördlich von Jakutsk . . ."

Macrorhamphus griseus . . . var. *scolopaceus*, Coues, 1873: no. 415a, part.

Macrorhamphus longirostris, Taczanowski, 1876:255. Cape Tchukotsk, Siberia.

Macrorhamphus griseus b. var. *scolopaceus*, Ridgway, 1880:159, part. Alaska, †Mississippi Valley.

Macrorhamphus griseus scolopaceus, Nelson, 1883:85. Kotzebue Sound, Bering Sea; Cape Wankarem, northeastern Siberia.

Macrorhamphus griseus scolopaceus, Dutcher, 1884:32. Shinnecock Bay, Long Island, N.Y.

Scolopax grisea, Seebohm, 1884:33. East Yezo I. and † Yokohama, Japan.

Ereunetes griseus, Seebohm, 1885:168, part. Alaska; Tchuski Land, northeastern Siberia; East Yezo, Japan,** the last based on a specimen collected on October 13, 1874, now in the U. S. Nat. Mus.

E[reunetes]. *griseus scolopaceus*, Seebohm, 1885:171, part. Pacific coast, Alaska to Mexico.

Macrorhamphus scolopaceus, Turner, 1886:146. St. Michael's,* St. Michael's I.,* Yukon Delta,* † Kuskokwim R., Alaska.

Macrorhamphus scolopaceus, Nelson, 1887:100. Norton Sound, Yukon Mouth,* Point Barrow,* Alaska.

Macrorhamphus griseus var. *scolopaceus*, Palmen, 1887:302. Jinretlen, Pitlekaj, northeastern Siberia.

- Macrorhamphus scolopaceus*, MacFarlane, 1891:426. Anderson River region, northwestern Mackenzie.
- Macrorhamphus griseus*, Poynting, 1895-1896:123. Anderson River Fort, Mackenzie.
- Macrorhamphus griseus*, Sharpe, 1896:396, part. Point Barrow and St. Michael, Alaska; British Columbia; De Soto Co., Fla.; Texas; Arizona; Zacatecas, Mexico.
- Macrorhamphus griseus scolopaceus*, Howe, 1901a:161, part. Alaska; Pacific coast; Sable I., N.S.;** southward along Atlantic coast; Florida.
- Macrorhamphus scolopaceus*, Fleming, 1906:449. Toronto** and Hamilton,** Ont.
- Macrorhamphus scolopaceus*, Goldman, 1908:203. Tulare Lake,** Calif.
- Macrorhamphus scolopaceus*, Preble, 1908:319. † Fort Simpson, † Fort Norman, Mackenzie; † La Pierre House, Y.T.
- Macrorhamphus griseus scolopaceus*, Cooke, 1910:28, part. Point Barrow,* Norton Sound, St. Michael,* mouth of Yukon,* Alaska; northern coast of eastern Siberia; Japan; Chilli-wack,* B.C.; Souris R.,* N.D.; Hamilton,* Ont.; Cape May,* N.J.; various localities on Gulf coast and in Mississippi Valley; Mimbres,* Ariz.; San Mateo,* Oaxaca; Guatemala.
- Macrorhamphus griseus scolopaceus*, Hathaway, 1913:551. Point Judith, R.I.
- Macrorhamphus griseus scolopaceus*, Anderson, 1913:472. Downy young near mouth of Kuparuk R., northern Alaska; Mackenzie delta.
- Macrorhamphus griseus scolopaceus*, Willett, 1918:85. Forrester I.,** Alaska.
- Macrorhamphus griseus scolopaceus*, Grinnell, Bryant, and Storer, 1918:358, part. Santa Ana,** Wilmington,** Los Banos,** Tulare Lake,** † 9 mi. E. Daggett, † Kern Lake, Calif. MVZ specimen 22232 shown in fig. 361 is a female of *scolopaceus* collected at Los Banos.
- Limnodromus griseus scolopaceus*, Ridgway, 1919:201, part. Northwestern Mackenzie; western Alaska; northeastern Siberia; Sinaloa (Mazatlan*); Oaxaca (San Mateo*); Guatemala; Nantucket,* Mass.; Point Judith, R.I.; Long Island,* N.Y.; Cape May,* N.J.; Georgia; Florida; Louisiana; Japan. All other localities given in Ridgway's statement of range (pp. 201-202) have not been verified, and some obviously represent *L. griseus*.
- Macrorhamphus griseus scolopaceus*, Hanna, 1920:173. St. Paul I.,* Alaska.
- Limnodromus griseus scolopaceus*, Preble and McAtee, 1923:66. St. Paul I.,* Pribilof Is., Alaska.
- Limnodromus griseus scolopaceus*, Brooks and Swarth, 1925:41. Okanagan,* Queen Charlotte Is.,* and Vancouver I.,* B.C.
- Limnodromus griseus scolopaceus*, Bent, 1927:121, part. † Franklin Bay, Mackenzie; † La Pierre House, Y.T.; all other breeding localities cited apply here. Records of migrant and winter occurrence apply variously to *L. scolopaceus* and *L. griseus*; a number of records of "early fall migrants" are those of nonbreeders.
- Limnodromus griseus scolopaceus*, Taverner, 1928:134. Mouth of Yukon River,* Alaska.
- Limnodromus griseus scolopaceus*, Grinnell, 1928:90, part. La Grulla,** Baja Calif.
- Macrorhamphus griseus scolopaceus*, Pleske, 1928:240. Jinretlen, Pitlekaj, and Cape Van-karema, on the Chukchi Peninsula, northeastern Siberia.
- Limnodromus griseus scolopaceus*, A.O.U. Check-list Committee, 1931:122, part. Point Barrow,* mouth of Yukon,* northwest Mackenzie; Florida; Louisiana; California; Mississippi Valley; Sable I.,* N.S.; Siberia; Japan. "Cuba" and "Jamaica" cannot be verified, since I have examined no skins of any dowitcher from these islands.
- Limnodromus scolopaceus*, Rowan, 1932:21, 25. Anderson River, Mackenzie, west to Point Barrow* and south to mouth of Yukon River* and Hooper Bay*; all localities listed (pp. 80, 31) except Big Lake, Alta., verified by specimens examined by me.
- Limnodromus griseus scolopaceus*, Willett, 1933:66, part. Wilmington* and Santa Ana,* Calif.; remaining localities cited under this name probably refer to *L. g. caurinus*.
- Limnodromus griseus fasciatus* Brodtkorb, 1933:124, part. Type, adult female, no. 3693, collection of H. B. Conover, collected at Hooper Bay, Alaska, on June 9, 1924, by H. B. Conover, original number 879. Measurements: wing 144 mm., culmen 73.2, tarsus 39.3. Localities cited and here considered to represent *scolopaceus*: Hooper Bay,* Kashunuk R.,* and Nome,* Alaska. Remaining localities cited under *scolopaceus* but here not considered to represent that species are given in the synonymies of the other forms.

Limnodromus griseus griseus, Brodtkorb, 1933:126, part. Sumas Lake,* B.C.

Limnodromus griseus scolopaceus, Bailey, Brower, and Bishop, 1933:27. Barrow* and Wainwright,* Alaska.

[*Limnodromus*] *scolopaceus*, Brooks, 1934:23. Pacific coast; erroneous claim of nesting at Churchill, Man.

Limnodromus griseus scolopaceus, Swarth, 1934:33. Nunivak I.,** Alaska.

Limnodromus griseus scolopaceus, Peters, 1934:272, part. Mouth of Yukon* and Point Barrow,* Alaska; † Franklin Bay, Mackenzie; central California; Mississippi Valley, Gulf states, and Florida; Atlantic coast; eastern Asia. No specimens examined by me from Cuba or Jamaica.

[*Limnodromus* † *g.*] *scolopaceus*, Taverner, 1935:15. Vicinity of Bering Sea; Alaska; British Columbia; southern central Canadian provinces.

Limnodromus griseus scolopaceus, Campbell, 1935:81. Erie Twp.,** Monroe Co., Mich.

Limnodromus griseus scolopaceus (*sic*), Twomey, 1936:130. Alaska; California; Texas.

[*Limnodromus griseus*] *scolopaceus*, Shortt and Waller, 1937:23. Fall migrant at Lake St. Martin,** Man.

Limnodromus griseus scolopaceus, Friedmann, 1938:88. Gambell,* St. Lawrence I., Alaska.

[*Limnodromus*]. *g*[*riseus*]. *scolopaceus*, Sutton, 1938:503. 3 mi. S Gate, Beaver Co., Okla.

Limnodromus griseus scolopaceus, Orr, 1940:63. Yukon delta;* 1 mi. W Pierce,** Solano Co., and Merced Co.,** Calif.

[*Limnodromus griseus*] *griseus*, Orr, 1940:63, part. Merced Co., Calif., October 29—a female specimen examined by me, called "*griseus*" by Orr because culmen length was less than 68 mm.; my measurements are: wing 146 mm., culmen 67.1 mm., tarsus 41.0 mm.; plumage is that of first-year *scolopaceus*.

Limnodromus griseus griseus, Sperry, 1940:15, part. Siberia. Citation of this locality under *L. g. griseus* by Sperry is based on Bent's (1927:115) listing of a supposed vagrant occurrence near Yakutsk, northeastern Siberia. The latter originated with Taczanowski (1873:112), who mentions the region of northeastern Siberia and, in my opinion, merely adds "north of Yakutsk" to orient the reader. Neither Ridgway (1919) nor Pleske (1926) lists this record.

Limnodromus griseus scolopaceus, Sperry, 1940:19, part. Point Barrow,* mouth of Yukon,* northwestern Mackenzie; Bear River,** Utah.

Limnodromus griseus scolopaceus, Swenk, 1940:65. Nebraska; Alaska and northwestern Mackenzie.

Limnodromus griseus scolopaceus, Conover, 1941:377. † Franklin Bay, Mackenzie; Point Barrow,* Hooper Bay,* Point Dall, St. Paul I.,* Nome,* Alaska; British Columbia; Alberta, Saskatchewan; Colorado; † Connecticut; California; Texas; Illinois; † North Carolina; Lower California. Conover (p. 378) correctly doubts assignment of Ecuadorian and West Indian specimens to this form.

Limnodromus griseus scolopaceus, Grinnell and Miller, 1944:147, part. Pierce,** Los Banos,** Salton Sea,** Fresno, † San Clemente I., † Daggett, † Tomales Bay, † Cygnus, all in California.

[†] *Limnodromus griseus scolopaceus*, Zotta, 1942:171. Record of a female in "summer" plumage taken at Santo Domingo (36°, 40' S, 58°, 25' W), Province of Buenos Aires, Argentina, Oct. 25, 1942; bill length, 69.5 mm.; now no. 6168a, Museo Argentino de Ciencias. Identification doubtful at present, since data are incomplete. The figured specimen is not one in full winter plumage as might be expected from the date of collection; it may be one in postjuvinal or abnormally protracted postnuptial molt, or in some peculiar mixture of plumages. The text description was recorded without regard to distinct plumages and plumage sequence. The bar pattern of the tail (figured) supports Zotta's identification, but neither this character nor that of bill length wholly excludes the possibility that it may be *L. g. hendersoni* or *L. g. caurinus*. His specimen should be examined by someone with access to comparative material. Data on chord of wing and tarsal length, together with the culmen measurement, might settle the question of identity.

I find no authentic record of *scolopaceus* south of Guatemala. The puzzling specimen reported by Zotta was a lone individual in a mixed flock of shore birds. There is no evidence at present that it represents any more than a vagrant occurrence, whatever the form involved.

Limnodromus griseus scolopaceus, Brandt, 1943:387. Hooper Bay,* Alaska.

Limnodromus scolopaceus, Belle, 1944:73. States that most Utah dowitchers are of this form. My records confirm this.

Limnodromus scolopaceus, van Rossem, 1945:84. Animas Valley,** N.M.; Ciudad Obregón, Las Carpas,** Sonora.

Limnodromus scolopaceus, Hellmayr and Conover, 1948:140, part. Localities not considered to represent *scolopaceus* are listed elsewhere in synonymies.

Specimens examined.—Total, 1,298, divided as follows: (1) Merced County, Calif., 311 (see table 6); (2) California, exclusive of Beck's sample of 311 from Merced County, 310 (see table 7); (3) Alaska, 187 (see table 16); (4) interior Canada, 121 (see table 17); (5) northeastern Atlantic coast, 61 (see table 18); (6) other parts of Canada and the United States, also Mexico, Guatemala, eastern Siberia, and Japan, 308.

1) CALIFORNIA. *Merced County*: Dos Palos,† 3; Gustine,† 11; Los Banos,† 17; Merced,† 280.

2) CALIFORNIA. *Alameda County*: Alameda,† 4; Alvarado,† 2; 4 mi. SW Alvarado,† 1; Hayward,† 8; 2½ mi. SSW San Leandro,† 1; unspecified, 3. *Contra Costa County*: 4 mi. NE Oakley,§ 1. *Humboldt County*: Big Lagoon,† 1; Eureka,† 1. *Imperial County*: 8 mi. NW Calipatria,† 4; 2 mi. W Niland,† 7. *Kern County*: 15 mi. NW Bakersfield,† 1; Buena Vista Lake,† 1. *Kings County*: Tulare Lake,† 1. *Los Angeles County*: Alhambra,§ 1; Nigger Slough,§ 13; San Pedro,† 1; Wilmington,† 1. *Marin County*: Novato,§ 1; Olema,§ 2. *Merced County*: Gustine,† 2; Los Banos,† 57; Merced,† 105; Planada,† 1; unspecified, 45. *Orange County*: Bolsa Chica,† 1; Santa Ana,§ 1. *Riverside County*: 1 mi. S Mecca,† 3; Riverside,† 1. *San Diego County*: Lake Hodges,§ 1; Pacific Beach,† 1; National City,† 1. *San Francisco County*: San Francisco,† 2. *San Joaquin County*: Stockton,† 2; 6 mi. NW Stockton,† 1. *San Mateo County*: Menlo Park,† 2; Redwood City,† 1. *Santa Clara County*: Alviso,† 11; ½ mi. N Alviso,† 1; Berryessa,† 1; Palo Alto,† 3. *Santa Cruz County*: Santa Cruz,† 4. *Solano County*: 1 mi. W Pierce,† 1. *Sonoma County*: Bodega Bay,† 4. *Yolo County*: Davis,† 3.

3) ALASKA. Alaktak [=Alagnak] R., 2; Barrow, 44 (see also Point Barrow); Bear Creek, 1; Cape Lisbourne, 3; Cape Nome, 10; Cape Prince of Wales, 5; Chipp R., 7; Colinson Point (250 mi. E Barrow), 1 (also 4 downy young); Dease Inlet (35 mi. E Barrow), 2; Forrester I., 1; Fort Yukon, 1; Gambell, St. Lawrence I., 2; Goodnews Bay, 1; Herschel I., 2; Hooper Bay, 10 (also 6 downy young); Kashunik R. (30 mi. from coast at Hooper Bay), 1; Kutleet [=Kotlik] R., 1; Nome, 6; Nunivak I., 2; Pastotie [=Pastolik] R., 2; Point Barrow, 20 (also 1 downy young); (Point Tangent, 2 downy young); Port Clarence, 1; Port Safety, 1; Resurrection Bay, 1; St. Michael, 16; St. Michael I., 2; St. Paul I., 3; Seal Bay (N side Alaska Pen.) [near Seal I. †], 1; Sitka, 1; Stikine mouth, Sergeif I. bar, 4; Tigara, Point Hope, 4; Walnwright, 4; Wales, 1; Yukon, 2; Yukon Delta, 6 (also 1 downy young); unspecified, 2.

4) ALBERTA. Athabaska delta (3 mi. above main branch), 1; Banff, 1; Beaverhill Lake (Tofield), 47; Beaver Lake, 3; Belvedere, 2; Camrose, 5; Didsbury, 2; Driedmeat Lake, 1; Edmonton, 5; Lac la Nonne, 5; Langdon, 1; Metiskow, 2; Pakowka Lake, 3; Rosebud, 3; Tofield (see Beaverhill Lake).

MANITOBA: Lake St. Martin Reservation, 4; Oak Lake, 10; Whitewater Lake (Regent), 2. SASKATCHEWAN: Dundurn, 8; Lake Johnson, 5; Last Mountain Lake (E of Imperial), 2; Liberty, 1; Maple Creek, 4; Watertown (near Davidson), 2; Wauchope, 1; Yorkton, 1. 5) EASTERN COAST. NOVA SCOTIA: Sable Island, 1 (Oct. 31).

FLORIDA. *Brevard County*: Banana Creek, 1 (March 10); Canaveral, 1 (April 15); East Peninsula, opp. Micco, 1 (March 5); Indian River, 2 (April 4-10). *Escambia County*:

† Fresh-water inland locality.

‡ Brackish or salt-water coastal locality.

§ Fresh-water coastal locality.

Pensacola, 1 (Oct. 21). *Glades County*: Citrus Center, 1 (April 20); Lake Hicpochee, 1 (April 19). *Monroe County*: Florida Keys, 3 (Dec. 3). *Okeechobee County*: Bassenger, 3 (March 1). *Polk-Osceola counties*: Kissimmee Lake, 5 (Feb. 15–April 16). *Osceola County*: Kissimmee, 9 (Feb. 15–April 16). *County?*: Puzzle Lake, St. Johns River, 2 (April 10); Upper St. Johns River, 1 (Dec. 24). Unspecified, 1 (no date).

GEORGIA. County unspecified, 1 (no date).

MASSACHUSETTS. *Barnstable County*: Cape Cod, 1 (Sept. 8); Orleans, 1 (Oct. 14). *Essex County*: Ipswich, 1 (Sept. 16); Newburyport, 2 (July 23, Sept. 15). *Nantucket County*: Nantucket I., 1 (Aug. 29). *Plymouth County*: Marshfield, 1 (Aug. 19).

NEW HAMPSHIRE. *Rockingham County*: Rye Beach, 1 (Aug. 2); Seabrook, 1 (Oct. 4).

NEW JERSEY. *Cape May County*: Cape May, 2 (May?; May 10, an unquestioned adult probably in migration). *County?*: Squaw Beach, 1 (Aug. 9). Unspecified, 1 (no date).

NEW YORK. *Nassau County*: Seaford, 1 (Aug. 14). *Queens County*: Rockaway, 4 (Aug. 7; Aug. 7; Sept. 27; Oct. 10). *Suffolk County*: Atlanticville, 1 (Aug. 7); Good Grounds, 6 (July 23–Sept. 26). County undetermined: Long Island, 1 (no date).

SOUTH CAROLINA. Turtle I., 1 (Nov. 30).

6) BRITISH COLUMBIA. Atlin, 1; Canoe Pass, Fraser R. mouth, 3; Chilliwack, 5; Fort Steele (Bummer's Flats), 7; Lulu I., Fraser R. delta, 13; Moresby I., 1; New Westminster, 1; Okanagan, 2; Okanagan Landing, 14; Ootsa Lake, 1; 149-mile Lake (E of Williams), 2; Rawlings Lake, 1; Sea I., 1; Sumas, 1; Sumas Prairie, 1; Sumas Lake, 8; unspecified, 1; *Queen Charlotte Islands*: Masset, 3. *Vancouver Island*: Comox, 4; Seal I., near Comox, 1.

ONTARIO. Hamilton, 1; Toronto, 1.

ARIZONA. *Cochise County*: Mimbres, 1.

COLORADO. *Adams County*: Barr, 1; Barr Lake, 1.

ILLINOIS. *Adams County*: Lima Lake, 1. *Henry County*: Swan Lake, 1. *McHenry County*: Cary Station, 1. *Wabash County*: Mt. Carmel, 1.

IOWA. County unspecified, 1.

KANSAS. *Coffey County*: Burlington, 2. *Pawnee County*: Larned, 1.

LOUISIANA. *Cameron Parish*: Cameron, 2. *Vermillion Parish*: Unspecified, 1.

MICHIGAN. *Bay County*: 3 mi. N Linwood, 1. *Monroe County*: Erie Twp., 11.

MONTANA. *Musselshell County*: Musselshell, 1.

NEBRASKA. *Douglas County*: Omaha, 1. *Garden County*: Unspecified, 1.

NEVADA. *Churchill County*: Carson Sink, 4.

NEW MEXICO. *Dona Ana County*: Las Cruces, 1. *Hidalgo County*: Animas Valley, 1. *Otero County*: White Sands Nat. Mon., 1. *San Miguel County*: San Miguel, 3.

NORTH DAKOTA. *Ramsey County*: Sweetwater, 1. *Towner County*: Unspecified, 1. *Walsh County*: Grafton, 18. *County?*: Souris River, 8. Unspecified, 1.

OREGON. *Crook County*: GI Ranch, 2. *Harney County*: Malheur Lake, 3; Narrows, 3; unspecified, 1. *Multnomah County*: Sauvies I., 3.

SOUTH DAKOTA. *Clay County*: Vermillion, 2. *Sanborn County*: Unspecified, 3.

TEXAS. *Araucarias County*: Rockport, 2. *Calhoun County*: Seadrift, 3. *Cameron County*: Brownsville, 38; Santa Maria, 1; unspecified, 2. *Kinney County*: Fort Clark, 1. *Lubbock County*: 1 mi. N Lubbock, 3. *McLennan County*: Lake Waco, 1. *Nueces County*: Corpus Christi, 3. *Refugio County*: Tivoli, 7. *San Patricio County*: Unspecified, 1. County unspecified, 1.

UTAH. *Box Elder County*: Mouth Bear River, 26. *Kane County*: 3 mi. S Kanab (4,850 ft.), 1. *Utah County*: Provo, 1. *Weber County*: Ogden, 8.

WASHINGTON. *Grant County*: Moses Lake, 2. *Grays Harbor County*: Westport, 1. *Pierce County*: Ft. Steilacoom, 1; Puyallup, 3. *Yakima County*: North Yakima, 1.

WISCONSIN. County unspecified, 1.

MEXICO. BAJA CALIFORNIA. Gardner's Lagoon, Salton River, 4; La Grulla, 7,200 ft., Sierra San Pedro Martir, 1; San Jose, 1; San Jose del Cabo, 2; Todos Santos, 1. CHIAPAS. Belen, Ulapa, 1; Las Garzas, Acepetahua, 5. CHIHUAHUA. Colonia Diaz, 3; Lake Palomas, Mimbres Valley, 6. JALISCO. La Barca, 2. OAXACA. San Mateo, Tehuantepec, 4. SINALOA. Mazatlan, 1. SONORA. Las Carpas, Colorado R., 5; Santa Ana, 62 mi. S Nogales, 1. VERA CRUZ. Mirador, 1.

GUATEMALA. Unspecified, 2.

SIBERIA. Chukchi Peninsula, 1.

JAPAN. Achi-Shibito, East Yezo I., 1.

Limnodromus griseus griseus (Gmelin)

[*Scolopax*] *grisea* Gmelin, 1789:658, original description. Type locality, coast of New York. Description based on the "Brown Snipe" of Pennant, 1785:464.

[*Scolopax*] *nutans* Gmelin, 1789:659. Type locality, Chateaux Bay, Labrador. Description based on the "Nodding Snipe" of Pennant, 1785:465, the juvenile of *L. g. griseus*.

[?] [*Scolopax*] *cayennensis* Gmelin, 1789:661. "Cayenna."

[?] [*Tringa*] *noveboracensis* Gmelin, 1789:673. New York. Description based on the "New York Sandpiper" of Pennant, 1785:474.

Scolopax leucophaea (not of Latham), Vieillot, 1816:358. Status of supposed type in British Museum, specimen no. 1889:5:30:19, is doubtful (J. R. Macdonald, letter).

Totanus ferrugineicollis Vieillot, 1816:401. New York.

Totanus griseus, Vieillot, 1816:406. Environs of New York City.

Macrorhamphus griseus, Leach, 1816:31. † Devonshire, England.

Scolopax paykulli Nillson, 1821:106. Lappland (=Sweden). See Swainson and Richardson, 1831:398. Type, a specimen in postjuvenile molt, in Stockholm Museum (Gyldenstolpe, 1927:101).

Macrorhamphus punctatus Lesson, 1831:556. New York; † northern Europe.

Limnodromus noveboracensis, Maximilian, 1832:717. Brazil.

Limnodromus griseus, Lembeye, 1850:91. Cuba.

Macrorhamphus noveboracensis, Lichtenstein, 1854:93.

Macrorhamphus griseus, Coues, 1861:229. Henley Harbor,* Labrador.

Macrorhamphus griseus, Lawrence, 1862:273. Cuba.

Limosa grisea, Schlegel, 1864:26.

Macrorhamphus griseus a. var. *griseus*, Ridgway, 1880:158, part. Atlantic coast.

Macrorhamphus griseus, Turner, 1885:246. Fort Chimo** and Davis Inlet, Ungava.

Ereunetes griseus, Seeborn, 1885:68, part. † Greenland; Atlantic coast; † West Indies.

Macrorhamphus griseus, Sharpe, 1896:396, part. Nova Scotia; Massachusetts; Brazil. Records from several localities in England presumably represent *L. g. griseus*, but no specimens from that country have been examined by me.

Macrorhamphus griseus, Howe, 1901a:158, part. Ungava.

Macrorhamphus griseus, Cooke, 1910:27, part. † Firkenaes, Greenland; Atlantic coast of Canada; New England states south to Cape Cod.

Limnodromus griseus griseus, Ridgway, 1919:197, part. Ungava, northern Labrador; Atlantic coast; southern Florida; Bahama Is. All other localities given in Ridgway's statement of range (p. 198) either have not been verified or appear in the synonymies of other races.

Limnodromus griseus griseus, Bent, 1927:114, part. Fort Chimo, Ungava; Atlantic coast; Brazil.

Limnodromus griseus griseus, Taverner, 1928:134, part. Atlantic coast of Canada.

Limnodromus griseus griseus, A.O.U. Check-list Committee, 1931:122, part. † Greenland; Canadian maritime provinces; † Bermuda; Brazil; † British Isles; † France.

L[imnodromus]. griseus griseus, Bowan, 1932:23. Toronto,** Ont.; Nova Scotia; New Brunswick; Massachusetts; Virginia; North and South Carolina; Georgia; Florida. All localities listed from specimens (pp. 34, 35) verified by me with exception of Macintosh Bay, Ga.

Limnodromus griseus griseus, Austin, 1932:101. Cites early records from Fort Chimo,** Quebec; Henley Harbor** and Davis Inlet, Labrador.

Limnodromus griseus griseus, Brodtkorb, 1933:126, part. Maranhão,** Brazil; all Massachusetts localities cited.* Remaining localities cited by Brodtkorb under this name but not considered to represent *L. griseus griseus* are given in the synonymies of the other races.

Limnodromus griseus griseus, Peters, 1934:272, part. Eastern Brazil.

[*Limnodromus griseus*] *griseus*, Taverner, 1935:15. ♀ Interior of Ungava.

Limnodromus griseus griseus, Gross, 1937:25. Turnavik West,** Labrador.

Limnodromus griseus griseus, Sperry, 1940:15, part. ♀ Greenland; Atlantic coast; central coastal Brazil.

Limnodromus griseus griseus, Witherby, et al., 1940:209, part. British Isles. Breeding range given (p. 211) is that of *L. g. hendersoni*. Winter ranges given (p. 211) apply overlappingly to all three races of *L. griseus*; the only localities given that could apply to *L. scolopaceus* are Central America and Pacific coast.

Limnodromus griseus griseus, Swenk, 1940:65, 69.

Limnodromus griseus griseus, Conover, 1941:380, part. James Bay,* Nova Scotia, Massachusetts, Connecticut, New York, North Carolina, South Carolina, Georgia, Florida, Virgin Is., Brazil (Maranhão**). (See also Hellmayr and Conover, 1948:144.)

Limnodromus griseus subsp. ♀ (*griseus* or *hendersoni*)

Macrorhamphus griseus, Cooke, 1910:27, part. Atlantic coast localities south of Long Island.

Limnodromus griseus griseus, A.O.U. Check-list Committee, 1931:122, part. Virginia, North Carolina, Florida, West Indies.

Limnodromus griseus fasciatus Brodkorb, 1933:124, part. Inagua,** Bahama Is.

Limnodromus griseus griseus, Brodkorb, 1933:126, part. Scattered Atlantic coast localities.

Limnodromus griseus griseus, Peters, 1934:272, part. Atlantic coast.

Limnodromus griseus griseus, Sperry, 1940:15, part. Atlantic coast; North Carolina, Florida, West Indies.

Limnodromus griseus griseus, Bent, 1927:114, part. Numerous localities on Atlantic coast south of Cape Cod and on eastern West Indies.

Limnodromus griseus hendersoni Rowan

[♂] [*Scolopax*] *noveboracensis* Gmelin, 1789:658. Type unknown. Type locality, coast of New York. Description based on "Red-breasted Snipe" of Pennant, 1785:464: "Bill . . . two inches one-eighth long: . . . under side of the neck and breast ferruginous, thinly spotted with black . . ." [italics mine]. This description suggests *hendersoni* more so than the nominate race, but no conclusive argument for the application of Gmelin's name can be developed. Thus, color of remaining under parts, a critical detail, is not given.

Totanus noveboracensis, Sabine, 1823:687. Dimensions reported are: bill $2\frac{1}{4}$ inches, tarsus $1\frac{1}{4}$ inches. These were taken from the "larger" of two specimens available to Sabine, and thus point to a race of *L. griseus*. The text of the report containing Sabine's paper as well as the species listed in the latter indicate that the specimens probably came from interior Canada, and for that reason Sabine's binomial is placed here.

[♂] *Scolopax noveboracensis*, Swainson and Richardson, 1831:398. Saskatchewan plains.

[♂] *Macrorhamphus griseus*, Kneeland, 1857:238. Keweenaw Point, Mich.

[♂] *A* [*scolopax*]. *noveboracensis*, Maximilian, 1859:93. Missouri.

Macrorhamphus scolopaceus, Lawrence, 1862:272. Texas, Cuba. The specimens in full summer plumage described are obviously those of *L. g. hendersoni*: "breast and entire abdomen are of a uniform rather pale rufous without spots or bars, but having the sides of the breast barred transversely with black" (p. 273). The author points out that "in *scolopaceus* the bill is longer, measuring in different examples [evidently not in those here reported upon] from $2\frac{3}{4}$ to 3 inches."

[*Macrorhamphus griseus*] *b.* var. *scolopaceus*, Ridgway, 1880:159, 160, part. No localities mentioned, but descriptions given indicate that specimens of *hendersoni* were mixed in with those of *scolopaceus*.

Macrorhamphus griseus, W. E. Clarke, 1890:321. Fort Churchill,* Man.

Macrorhamphus griseus, Sharpe, 1896:396, part. ♀ Rockford, Illinois; ♀ Corpus Christi, Texas; ♀ Tarpon Springs, Fla.; ♀ Cedar Keys, Fla.

Macrorhamphus griseus, Howe, 1901a:158, part. Atlantic coast of Carolinas.

M [*acrorhamphus*]. *g* [*riseus*]. *scolopaceus*, Howe, 1901b:272. Button Bay [=North R., 10 mi. NW Churchill],** Man.

- Macrorhamphus scolopaceus*, Preble, 1902:95. Fort Churchill,* Man. I agree with Rowan (1932:25) that this is a record of *L. g. hendersoni*.
- Macrorhamphus scolopaceus*, Preble, 1908:319. Big Island** and Fort Rae,** Mackenzie.
- Macrorhamphus scolopaceus*, Macoun and Macoun, 1909:166, part. Nesting in northern Alberta reported by Rainco. This reference is typical of many that include data on *L. scolopaceus*, *L. g. hendersoni*, and *L. g. caurinus* under the name of the first.
- Macrorhamphus griseus scolopaceus*, Cooke, 1910:28, part. Fort Anderson, Mackenzie; Fort Churchill,* Man.; also, probably most Mississippi Valley and Gulf coast localities given by Cooke belong here.
- Limnodromus griseus griseus*, Bent, 1927:113-114, part. Alberta; west side of Hudson Bay; Fort Rae, Mackenzie; Mississippi Valley; Gulf coast.
- [†] *Limnodromus griseus scolopaceus*, Ridgway, 1919:201, part. West Indies.
- Limnodromus griseus griseus*, Ridgway, 1919:197, part. Mississippi Valley; † northern Idaho.
- Limnodromus griseus*, Rowan, 1927:210, part. † "The Point" (=Blakeney Point, Norfolk), † Belvedere, Klondike City,* Alta.
- Limnodromus griseus griseus*, Taverner, 1928:134, part. 60 mi. NW Edmonton, Alta.; Canadian prairies.
- Limnodromus griseus scolopaceus*, Forbush, 1925:378, part. Description of adult in breeding plumage refers to *L. g. hendersoni*; hence Forbush's doubt about the validity of *scolopaceus*. The specimen of "*scolopaceus*" from Cape Poge, Mass., August 16, 1904, MCZ 315475, is a juvenal "male" with culmen length of 63.0 mm. Plumage characters are those of *L. griseus*. The specimen is probably missexed, and may be a female of *hendersoni*. None of the other listed specimens of "*scolopaceus*" has been examined by me.
- Limnodromus griseus griseus*, A.O.U. Check-list Committee, 1931:122, part. Central Alberta; Churchill,* Man.; † Idaho, etc.
- L[imnodromus]. griseus hendersoni* Rowan, 1932:22, original description, part. Type, a male collected on June 19, 1924, at Devil's Lake, Alta., by W. Rowan (*op. cit.*:32); now no. 24832 in the collection of the National Museum of Canada. Localities mentioned in statement of range: Lake Athabaska south to latitude 53°,* Alberta; Saskatchewan; Churchill,* Man.; Toronto,** Ont.; South Carolina. All localities listed (pp. 32, 33) verified by specimens examined by me with exception of Devil's Lake, Alta.
- Limnodromus griseus scolopaceus*, Murray, 1933:195. Bone I,** Va. Record based on two females collected on July 14, 1880: US 80274 represents *hendersoni*; US 80273 not examined.
- Limnodromus griseus griseus*, Brodtkorb, 1933:126, part. Localities applying here: all Alberta localities cited; * Osler,* Sask.; Andros,* Bahama Is.; probably all Virginia* and South Carolina* localities cited (see table 26); probably most localities cited from Mississippi Valley and Gulf coast (see p. 43).
- [*Limnodromus griseus*] *hendersoni*, Brooks, 1934:23, part. Central Alberta; Churchill,* Man.
- Limnodromus griseus*, Taverner and Sutton, 1934:44. Churchill,* Man.
- Limnodromus griseus griseus*, Peters, 1934:272, part. Lake Athabaska south to 53° N. lat., Alberta; Churchill,* Man.; Gulf states.
- [*Limnodromus griseus*] *hendersoni*, Taverner, 1935:15, part. Churchill,* Man.; western Alberta. Taverner's claim that *hendersoni* and *scolopaceus* are similarly colored indicates some misidentification of specimens.
- [*Limnodromus griseus*] *hendersoni*, Shortt and Waller, 1937:23. Lake St. Martin,** Man.; reported breeding.
- L[imnodromus]. g[riseus]. hendersoni*, Sutton, 1938:503. Gate, Beaver Co., Okla.
- Limnodromus griseus hendersoni*, Cowan, 1939:31. Tupper Creek, Peace River District, B.C.
- Limnodromus griseus griseus*, Sperry, 1940:15, part. Central Alberta; Osler,* Sask.; Churchill,* Man.
- Limnodromus griseus hendersoni*, Swenk, 1940:65, 67, 69. Nebraska; Alberta and Manitoba.

[?] [*Limnodromus griseus griseus*] "the true Eastern Dowitcher," Swenk, 1940:70. Lincoln, Lancaster Co., Neb., a male collected on September 7, 1932. The evidence given indicates that this could be, and more likely is, an extreme variant of *L. g. hendersoni*.

Limnodromus griseus hendersoni, Conover, 1941:379, part. Alberta, Manitoba, North Dakota, Illinois, North Carolina, South Carolina, Texas, ? Costa Rica. (See also Hellmayr and Conover, 1948:142.)

Limnodromus griseus hendersoni, Behle, 1944:73. Reports *hendersoni* less common in Utah than *scolopaceus*. My records confirm this.

Limnodromus griseus griseus, Todd, 1947:401. Last Mountain Lake** and Davidson,** Sask.

Limnodromus griseus subsp. ? (*hendersoni* or *caurinus*)

Macrorhamphus scolopaceus, Lawrence, 1868:141. Costa Rica.

Macrorhamphus griseus scolopaceus, Cooke, 1910:28, part. Costa Rica; Panama; Ecuador; Tumbes, Peru.

Limnodromus griseus scolopaceus, Ridgway, 1919:201, part. Costa Rica, Colombia, Ecuador.

Limnodromus griseus scolopaceus, Chapman, 1926:194. Vaqueria** and Tembleque I.,** Ecuador.

Limnodromus griseus griseus, Bent, 1927:114, part. Peru.

Limnodromus griseus scolopaceus, Bent, 1927:121, part. Costa Rica, Panama, Colombia, Ecuador.

Limnodromus griseus griseus, A.O.U. Check-list Committee, 1931:122, part. Peru.

Limnodromus griseus scolopaceus, A.O.U. Check-list Committee, 1931:122, part. Panama, Ecuador.

Limnodromus griseus fasciatus Brodkorb, 1933:124, part. Guanacaste,** Costa Rica.

Limnodromus griseus griseus, Brodkorb, 1933:126, part. Guanacaste,** Costa Rica; San Jose del Cabo,** Baja California.

Limnodromus griseus scolopaceus, Peters, 1934:272, part. Ecuador.

Limnodromus griseus griseus, Peters, 1934:272, part. Peru.

Limnodromus griseus griseus, Sperry, 1940:15, part. Peru.

Limnodromus griseus hendersoni, van Rossem, 1945:85. Mascori I., Agiabampo, and Tobarí Bay, Sonora.

Limnodromus scolopaceus, Hellmayr and Conover, 1948:141, 142, part. Peru; ? Cuba; ? Jamaica; Baja California.

Limnodromus griseus caurinus Pitelka

For original description, see page 43.

[?] *Scolopax grisea*, Ornithological Committee, 1837:193. Columbia River.

[?] *Scolopax grisea*, Newberry, 1857:100. Oregon; California.

Macrorhamphus griseus, Selater, 1859:237. Vancouver I., B.C.

Macrorhamphus scolopaceus, Nelson, 1887:100, part. No localities given are assignable to *caurinus*, but discussions of characters clearly indicates confusion of characters distinguishing *scolopaceus* from the species *griseus*; hence Nelson's use of the name given above applies to both forms. This confusion was noted by Brooks, 1934:23, who, however, is mistaken in stating that Nelson's comments apply only to "*hendersoni*," and thus by implication to the species *griseus*.

[?] *Macrorhamphus griseus*, Sharpe, 1896:396, part. ? British Columbia; ? San Juan I., Wash.

Macrorhamphus griseus scolopaceus, Osgood, 1901:74. Fort Kenai,* Alaska.

[?] *Macrorhamphus griseus scolopaceus*, Howe, 1901a:161, part. Pacific coast.

Macrorhamphus griseus, Osgood, 1904:62. Nushagak,** Alaska.

Macrorhamphus griseus scolopaceus, Cooke, 1910:28, part. Fort Kenai,* Alaska.

Macrorhamphus griseus scolopaceus, Swarth, 1911:49. Kuiu I.,** Alaska.

Macrorhamphus griseus scolopaceus, Willett, 1914:79. Kruzoff I.,* Alaska.

Macrorhamphus griseus scolopaceus, Grinnell, Bryant, and Storer, 1918:358, part. San Diego* and Santa Barbara,* Calif.

- Limnodromus griseus griseus*, Ridgway, 1919:197, part. Nushagak,** Alaska.
- Macrorhamphus griseus scolopaceus*, Brooks, 1920:28. Coast of British Columbia.**
- Macrorhamphus griseus scolopaceus*, Mailliard, 1921:31. Alameda,** Calif.
- Limnodromus griseus griseus*, Brooks and Swarth, 1925:128. Osoyoos,* B.C.
- Macrorhamphus griseus scolopaceus*, Bailey, 1927:193. Hooniah Sound,** Alaska.
- Limnodromus griseus scolopaceus*, Grinnell, 1928:90, part. "Brewster's Cape birds"*** from Baja California; San Felipe,** Baja California.
- Limnodromus griseus griseus*, Taverner, 1928:134, part. Pacific coast of Canada.
- Limnodromus griseus scolopaceus*, Grinnell and Hunt, 1929:67. Morro Bay,** Calif.
- Limnodromus griseus scolopaceus*, Grinnell, Dixon, and Linsdale, 1930:224. Near Dale's,** Tehama Co., Calif.
- Limnodromus griseus griseus*, Bent, 1927:114-115, part. Southern California; Nushagak,** Alaska.
- Limnodromus griseus scolopaceus*, Bent, 1927:121, part. Craig, and Kuiu I., Alaska; San Diego, Alameda, and Ballona, Calif.; etc.
- Limnodromus griseus griseus*, A.O.U. Check-list Committee, 1931:122, part. Alaska; Pacific coast.
- L[imnodromus]. griseus hendersoni* Rowan, 1932:22, 26, part. British Columbia; Los Angeles County,* Calif.
- Limnodromus griseus scolopaceus*, Hurley, 1932:17. Bristol Bay region (Kvichak River, Nakcen), Alaska.
- Limnodromus griseus fasciatus* Brodtkorb, 1933:124, part. Izembek Bay,* Alaska.
- Limnodromus griseus griseus*, Brodtkorb, 1933:125, part. Kuiu I.,** Alaska; all California localities cited.*
- Limnodromus griseus griseus*, Willett, 1933:66. Sunset Beach, Del Rey, Alamitos Bay,* southern California.
- Limnodromus griseus scolopaceus*, Willett, 1933:66, part. Santa Barbara,* Balboa, Playa del Rey,* San Diego Bay,* Calif.
- [*Limnodromus griseus*] *griseus*, Brooks, 1934:23, part. Pacific coast.
- [*Limnodromus griseus*] *hendersoni*, Brooks, 1934:23, part. Pacific coast.
- Limnodromus griseus griseus*, Peters, 1934:273, part. Southern California.
- [*Limnodromus griseus*] *hendersoni*, Taverner, 1934:15. British Columbia.
- [?] *Limnodromus griseus scolopaceus*, Friedmann, 1935:35. Kodiak I., Alaska.
- Limnodromus griseus*, Shortt, 1939:15. Yakutat;** muskegs near Situk River, Alaska.
- Limnodromus griseus griseus*, Orr, 1940:63, part. Point Reyes,** Calif. Specimens of the short-billed dowitcher studied by Orr represent in the majority, if not entirely, the Alaskan form, not "the inland breeding form."
- Limnodromus griseus griseus*, Sperry, 1940:15, part. Alaska.
- Limnodromus griseus hendersoni*, Conover, 1941:379, part. California. (See also Hellmayr and Conover, 1948:142.)
- Limnodromus griseus griseus*, Conover, 1941:380, part. California. (See also Hellmayr and Conover, 1948:144.)
- Limnodromus griseus hendersoni*, Jewett, 1942a:37. Astoria** and coast of Lincoln County,** Ore.
- Limnodromus griseus hendersoni*, Jewett, 1942b:79. Westport,** Wash.
- Limnodromus griseus hendersoni*, Slipp, 1943:198. Nisqually, Wash.
- Limnodromus griseus scolopaceus*, Grinnell and Miller, 1944:147, part. Tule Lake,** Calif.
- Limnodromus griseus griseus*, Grinnell and Miller, 1944:148. Arcata,** Dale's,** Lake Tahoe,** Point Reyes,** Alameda,** Los Banos,** Santa Cruz,** Moss,** Santa Barbara,** 8 mi. NW Calipatria,** all in California.
- Limnodromus griseus scolopaceus*, Gabrielson, 1944:125. Yakutat,** Alaska.
- [*Limnodromus griseus*] *griseus*, Aldrich, 1948:286, part. Pacific coast.
- [*Limnodromus griseus*] *hendersoni*, Aldrich, 1948:286, part. Pacific coast.
- Limnodromus scolopaceus*, Hellmayr and Conover, 1948:141, 142, part. Bristol Bay, Alaska; Motordrome,** Calif.

Specimens examined.—Total, 1,610, divided as follows: (1) California, 401 (see table 8); (2) Alaska, 47 (see table 23); (3) British Columbia, Washington, and Oregon, 139; (4) Alberta, Mackenzie, and Saskatchewan, 100 (see table 20); (5) Manitoba, 101 (see table 21); (6) eastern Canada and New England coast south to Massachusetts, 117 (see table 24); (7) Rhode Island, Connecticut, and New York, 71 (see table 25); (8) central Atlantic states, 173 (see table 25); (9) south Atlantic states, eastern West Indies, 165 (see table 25); (10) Gulf coast, Florida to Texas, 107 (see table 25); (11) interior states, 125; (12) Mexico, Central America, and northern South America, 64.

Limnodromus griseus caurinus

1) CALIFORNIA. *Alameda County*: Alameda, † 153; Bay Farm Island, † 4; Dumbarton Bridge, † 2; Hayward, † 5; 1½ mi. W Russell, † 1. *Contra Costa County*: El Cerrito, † 2; unspecified, 1. *El Dorado County*: Rowland's Marsh, Lake Tahoe, † 1. *Humboldt County*: 3 mi. W Arcata, † 1. Eureka, † 11; Trinidad, † 14. *Imperial County*: 8 mi. NW Calipatria, † 1. *Kern County*: 15 mi. NW Bakersfield, † 2. *Los Angeles County*: Alamitos Bay, † 8; Ballona, † 1; Motordrome, † 9; Playa del Rey, † 2. *Marin County*: Drake's Estero, 4 mi. WSW Inverness, † 1; Point Reyes, † 1. *Merced County*: Los Banos, † 9; Merced, † 4; unspecified, † 7. *Monterey County*: Carmel, † 11; mouth Carmel R., † 5; Monterey, † 2; Monterey Bay, † 3; mouth Salinas R., † 10; Moss Landing (including "Moss"), † 29; unspecified, 1. *Orange County*: Anaheim Landing, † 1; Seal Beach, † 1. *San Diego County*: National City, † 20; Long Beach, † 3; Pacific Beach, † 4; San Diego Bay, † 11; unspecified, 2. *San Joaquin County*: Stockton, † 1. *San Luis Obispo County*: Morro Bay, † 5. *San Mateo County*: Redwood City, † 4. *Santa Barbara County*: Carpinteria, † 2; Goleta, † 3; Santa Barbara, † 7. *Santa Clara County*: Alviso, † 20; ½ mi. N Alviso, † 1; Duddfield Flat (12 ft.), † 2. *Santa Cruz County*: Santa Cruz, † 5; ocean shore 1 mi. S Waddell Creek, † 1. *Siskiyou County*: Tule Lake, † 1. *Sonoma County*: Bodega Bay, † 1. *Tehama County*: 2 mi. N Dale's (700 ft.), † 2. *Ventura County*: Point Mugu, † 3.

2) ALASKA. Agashick [=Ugashik] Station, 1; Caamano Pt., Clarence Straits, 3; Chignik, 1; Cold Bay (Alaska Peninsula), 2; Craig, Prince of Wales I., 3; Hoonah Sound, 3; Igushik [R.], 1; Izembek Bay, 3; 22 mi. N Juneau (sea level), 4; Kenai, 2; Kruszoff I., 1; Knia I., 6; Nushagak, 1; 10 mi. above Nushagak, 1; Nushagak R., 2; Port Moller, 1; mouth Stikine R., 2; Ugashik R. (Alaska Peninsula), 1; Yakutat, 9 (including type of *L. g. caurinus*).

3) BRITISH COLUMBIA. Banks I., 2; Calvert I. (Safety Cove), 9; Denman I., 4; Discovery I., 2; Goose I., 6; Hakai Pass, 3; Head Kwakshua Pass (N arm), Calvert I., 3; Lone I., 1; Moresby I., 2; Osyoos, 2; Osyoos L., 8; Port Simpson, 1; Sea I., 2; Steveston, Lulu I., 1; Tatshenshini R. (Mile 85, Haines Rd.), 1. *Queen Charlotte Is.*: Masset, 26; unspecified, 1. *Vancouver I.*: Clayoquot, 1; Comox, 11; Cape Scott, 1; Seal I. (near Comox), 1; Sidney, 1; Tofino, 6; Upper Campbell Lake, 1.

WASHINGTON. *Grays Harbor County*: Copalis, 3; Ocosta, 1; Westport, 18. *King County*: Seattle, 1. *Pacific County*: Ilwaco, 2; Long Beach, 1; Tokeland, 1. *Pierce County*: Tacoma, 4.

OREGON. *Clatsop County*: Astoria, 6. *Lincoln County*: Newport, 4; Siletz Bay, 1; Yachats, 1.

Limnodromus griseus hendersoni

4) ALBERTA. Beaverhill Lake (Tosfield), 10; Beaver Lake, 4; Buffalo Lake, 1; Camrose, 8; 7 mi. W Edmonton, 2; Fawcett, 27 (+ 3 downy young); 8 mi. W Fawcett, 1; Flat Lake, 1; Fort Assiniboine, 3; Klondike City, 2; Lac la Nonne, 3; La Saline (Athabaska R.), 8; Poplar Point (near Athabaska L.), 1; Gov't Hay Camp, Slave R. (Wood Buffalo Park), 1; Little Red Deer R., Didsbury, 1.

MACKENZIE. Fort Rae (Great Slave L.), 1; Big I. (Great Slave L.), 1.

† Fresh-water inland locality.

‡ Brackish or salt-water coastal locality.

SASKATCHEWAN. Crooked Lake, 2; Davidson, 4; Dundurn, 1; Indian Head, 1; Last Mountain Lake (E of Imperial), 4; N. Montreal Lake, 4; Osler, 6.

5) MANITOBA. Fort Churchill (and "Churchill"), 65 (+ 12 downy young); North R., 10 mi. NW Churchill, 2; Gypsumville, 5; Halcrow L. (The Pas), 1; Lake St. Martin Reserve (near Gypsumville), 3; Shoal L., 7; West Kildonan, 1; Whitewater L. (Regent), 5.

Limnodromus griseus griseus

(Some fall-taken, first-year specimens of *L. g. hendersoni* are included. See text page 41.)

6) LABRADOR. Fort Chimo, 1; Henley Harbor, 1; West Turnavik Harbor, 1.

QUEBEC. Johan Beetz Bay, Saguenay Co., 1; Magdalen I., 1.

ONTARIO. Amherst I., 1; Nettichi R., James Bay, 1; Moose Factory, 1.

NEWFOUNDLAND. Stephenville Crossing, 2.

NOVA SCOTIA. Barrington, 4; Cape North, 1; Cheboque, 1; Crescent Beach, 9; Lunenburg County, 1; Wolfville, 2.

NEW BRUNSWICK. Grand Manan, Three Is., 13.

NEW HAMPSHIRE. *Rockingham County*: Atlantic, 1; Rye Beach, 6; South Seabrook, 2.

MASSACHUSETTS. *Barnstable County*: Barnstable, 1; West Barnstable, 1; Cape Cod, 3; Chatham, 11; East Orleans, 12; Great I., 2; Monomoy, 1; Monomoy I., 10; North Eastham, 1; Yarmouth, 1. *Dukes County*: Cape Poge, 1. *Essex County*: Newburyport, 4. *Nantucket County*: Gravel I., 1; Muskeget I., 1; Tuckernauck I., 2. *Norfolk County*: Cohasset, 2. *Plymouth County*: Marshfield, 8. County unspecified, 5 (including "Boston Market," 2).

Limnodromus griseus, subsp. *griseus* or *hendersoni*

7) RHODE ISLAND. *Newport County*: Middletown, 1; Newport, 2.

CONNECTICUT. *Middlesex County*: Grove Beach, 2. *New Haven County*: Guilford, 1; Madison, 1; New Haven, 1.

NEW YORK. *Nassau County*: Hempstead Bay, 3; Freeport, 1; Rockaway, 6; East Rockaway, 2; South Oyster Bay, 1; Seaford, 1; Short Beach, 5. *Suffolk County*: Amityville, 4; Bellport, 1; East Hampton, 1; Good Grounds, 18; Jones Beach, 1; Mastic, 3; Montauk Point, 1; Moriches, 1; East Moriches, 1; Oak Beach Flats, 1; Oak I., 2; Shinnecock Bay, 4; Speonk, 1; 3-mile Harbor, 1. *Long Island* (county undetermined): Meco Bay, 1; unspecified, 2. County undetermined: Paw I. Scholls, 1.

8) NEW JERSEY. *Cape May County*: Cape May, 4. *Ocean County*: Barnegat Inlet, 2. County undetermined: Squaw Beach, 2. County unspecified, 1.

VIRGINIA. *Accomac County*: Wachapreague, 4; Wallops I., 2. *Northampton County*: Bone I., 4; Cape Charles, 1; Cherrystone, 1; Cobb I., 23; Smith I., 6. *Princess Anne County*: Back Bay, 2.

NORTH CAROLINA. *Buncombe County*: Swaumanon, 1. *Brunswick County*: Cape Fear, 4. *Currituck County*: Currituck Light Beach, 22. *Dare County*: Rodie I., 25; Cape Hatteras, 2; Hatteras, 12; Kitty Hawk, 1; New Inlet, 5; Pea I., 47; Oregon Inlet Lighthouse, 1. *Warren County*: Fort Macon, 1.

9) SOUTH CAROLINA. *Beaufort County*: Fripp I., 1; Frogmore, 4; Sullivan I., 1. *Charleston County*: Bird Key, 7; Bull's Bay, 3; Cape I., 1; Charleston, 5; Christchurch Parish, 8; Oponhee Sound, 29; Dewee's I., 3; Long I. [=Isle of Palms], 1; McClellanville, 1; Mt. Pleasant, 18; Porcher's Bluff, 6; Porcher's Creek, 3; Price's Inlet, 1; Seabrooks I., 1; Sol Legare I. [near James I.], 1; Sullivan I., 4; Wayne's Place, 22.

GEORGIA. *Chatham County*: Savannah, 2; unspecified, 2. *McIntosh County*: unspecified, 4. *Glynn County*: St. Simon's I., 1.

FLORIDA. *Dade County*: Miami, 1. *Nassau County*: Amelia I., 13. *Volusia County*: Smyrna, 1.

WEST INDIES. *Antigua*: Long I., 1; Winthropes, 1. *Bahama Is.*: Andros I., 3; Great Inagua (Mathew), 2. *Grenadines* (Mustique I.), 2. *St. Vincent I.* (Brighton), 1. *Virgin Is.* (St. Croix), 11.

Limnodromus griseus hendersoni

(Specimens from the eastern Gulf coast and interior parts of the northeastern states and eastern Canadian provinces probably include some of *L. g. griseus*.)

10) FLORIDA. *Collier County*: Caxambox, 1; Marco, 3. *Escambia County*: Pensacola, 3. *Levy County*: Cedar Keys, 10. *Manatee County*: Indian Pass, 2. *Monroe County*: Cape Sable, 4; Florida Keys, 3; Pavilion Key, 3 (including 1 of *L. g. griseus*); Key West, 2. *Pinellas County*: Clearwater, 1; Gulfport, 4; Indian Rocks, 2; Passagrille, 3; Tarpon Springs, 3. *Wakulla County*: St. Marks, 11.

ALABAMA. *Mobile County*: Bayou Labatre, 1; Dauphine I., 8.

MISSISSIPPI. *Harrison County*: Biloxi, 10; Cat I., 3; Deer I., 7 (including 1 of *L. g.*

LOUISIANA. *Plaquemines Parish*: Breton I., 1. *Jefferson Parish*: Grand Isle, 1. Parish undetermined: Karaco Pass, 1.

TEXAS. *Aransas County*: Aransas Bay, 2; Rockport, 1. *Cameron County*: Padre I., 2. *McGlennan County*: Brazos R. near Waco, 1. *Nueces County*: Corpus Christi, 4; N end Padre I., 2. *Refugio County*: Tivoli, 1. *Nueces-San Patricio counties*: Corpus Christi Bay (Shamrock Point), 2. *San Patricio County*: Mustang I., 2; 1 mi. W Port Aransas, 1; unspecified, 2.

11) NEW YORK. *Seneca-Cayuga counties*: Cayuga Lake, 1.

PENNSYLVANIA. *Cumberland County*: Carlisle, 2.

ONTARIO. *Essex County*: Point Pelee, 1. *Norfolk County*: Long Point, 3. *York County*: Toronto, 10.

MICHIGAN. *Cheboygan County*: Duncan Bay, 1. *Chippewa County*: Munuscong State Park, 1. *Jackson County*: Portage Lake, 1. *Monroe County*: Erie, 1; 1½ mi. SSE Erie, 1; Erie township, 12. *Wayne County*: Ecorse, 2.

ILLINOIS. *Cook County*: Hyde Lake, 9; Calumet, 1. *Lake County*: Beach, 1; Deerfield, 1.

MINNESOTA. *Hennepin County*: Minneapolis, 1. *Lac Qui Parle County*: Unspecified, 2.

NEBRASKA. *Douglas County*: Omaha, 1.

LOUISIANA. *Ouachita Parish*: Monroe, 1.

NORTH DAKOTA. *Benson County*: Mauraise Bay, 2. *Nelson County*: Stump Lake, 12. *Ramsey County*: Sweetwater, 2. *Towner County*: Cando, 2; Rocklake, 2; unspecified, 1. *Walsh County*: Grafton, 44.

SOUTH DAKOTA. *Clay County*: Vermillion, 1. *Sanborn County*: unspecified, 5.

UTAH. *Box Elder County*: mouth Bear R., 1.

Limnodromus griseus, subsp. *caurinus* or *hendersoni*

12) BAJA CALIFORNIA. La Paz, 2; San Felipe, 1; San Lucas (15 mi. S Santa Rosalía), 2; San José del Cabo, 14; San Quintín, 1.

EL SALVADOR. Usulután, Puerto El Triunfo, 6.

COSTA RICA. Guanacaste (Punta Piedra, sea level), 8; Guanacaste (Piedra de Blanca), 5; Pt. Jiménez, Peninsula of Oso, Pacific side, 2.

PANAMA. Perme, 1.

COLOMBIA. Pizarro, Choco, 1.

ECUADOR. Esmeralda, 1; Tembleque I., 4; Vaqueria, 11.

PERU. Dept. Lima: Vegeta, 1.

BRAZIL. Mangunça I. (Maranhão), 2; Recife, 1; unspecified, 1 (all *L. g. griseus*).

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PLATES

PLATE 1

Ammodromus scolopaceus, in ventral view, showing increasing density of ventral spotting left to right. Specimens, left to right: first-year male, May 10, 1944 (MVZ 96969); adult female, May 13, 1944 (MVZ 96973); adult female, April 30, 1943 (MVZ 96914); adult male, April 28, 1944 (MVZ 96964); adult female, April 15, 1944 (MVZ 96951); first-year female, April 23, 1943 (MVZ 96906); all six specimens from Merced, California.

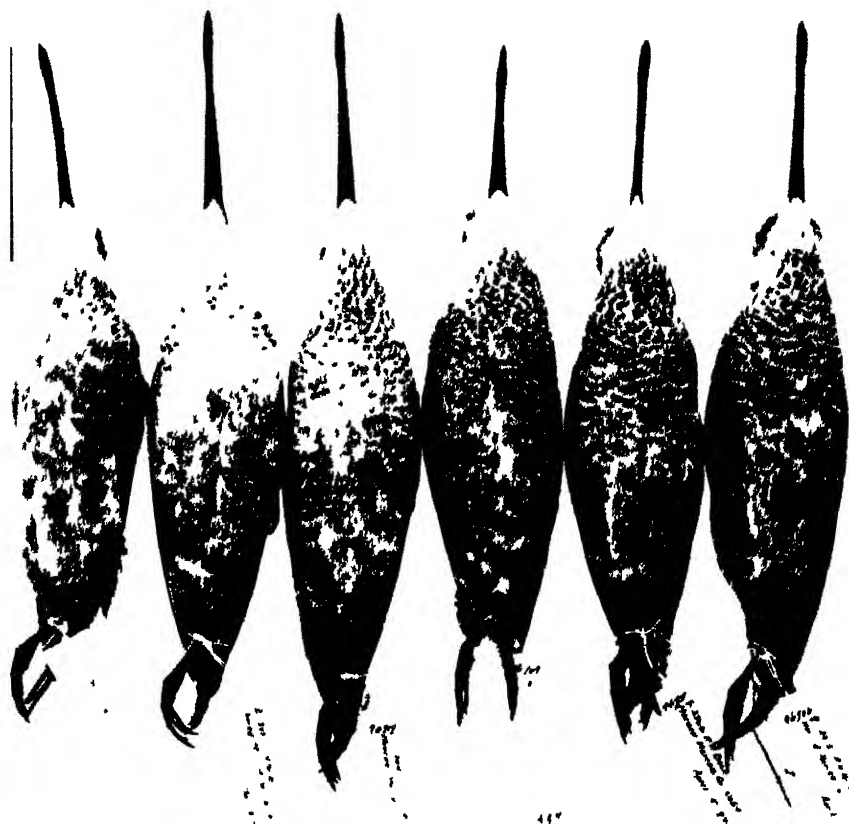


PLATE 2

Type series of *Immodiromus gris-uscanninus* showing variation in ventral color characters. Specimens bottom to top: male (adult) May 21, 1906 (ROM 691829) adult female May 14, 1906 (ROM 691824) male (adult) May 21, 1906 (ROM 691826) male (adult?) May 21, 1906 (ROM 691827) adult female type of *I. g. caninus* May 21, 1906 (ROM 691820) adult female May 21, 1906 (ROM 691828) all six specimens from Yakutat, Alaska.



PLATE

Specimens of *Limnodynastes* as exemplifying arbitrary classes of ventral spotting (table I). Specimens bottom to top: class A, adult female mouth Stelm. R. Alaska May 1, 1910 (CAS 60112) and adult female Comex. Vancouver I. I. C. May 1, 1911 (C 111491); class B, adult female Osoyoos I. I. C. May 7, 1922 (NM 1788) and adult female Churchill Man. July 12, 1911 (C 11098); class C, adult female Churchill Man. June 12, 1911 (C 11056) and adult female Churchill Man. June 20, 1911 (C 110588); class D, adult male Mussel I. C. May 7, 1920 (AB 1885) and adult male Alameda Calif. April 22, 1910 (CAS 1722). In ground color, specimen 1 (counting bottom to top) represents class b; specimens 1, 3, and 7 represent class c; specimens 2, 6, and 8 represent class d; and specimen 5 represents class e.



PLATE 4

Specimens showing closest observed approach of ventral coloration in *I. griseus* toward *I. scolopaceus*. Specimens 1 to 4 left to right represent *I. griseus*. Specimen 5 represents *I. scolopaceus*. Specimens left to right: adult female Alameda Calif. April 6, 1910 (C AS 17441) female (adult?), Denman I. B.C. May 1, 1911 (C 115480) female (first year?) Lofno B.C. May 11, 1911 (KR 557) adult female same place and date as last (KR 556) adult male Merced Calif. April 26, 1944 (MVZ 96962)



PLATE 5

Specimens of the snipe-billed godwit and dowitchers in breeding plumage shown in lateral view. Left to right: specimen 1 *Pseudoscolopax semipalmatus*, adult male, Ban Hui Sam, April 22, 1926 (CM 8071); specimens 2 and 3, *I. scolopaceus*, first year female, Okinagin, BC, May 19, 1930 (AB 1251) and first year male, Lost Mountain Lake, Sisk, May 12, 1932 (C 111962); specimens 4, 5 and 6, *I. griseus*, adult female, Alviso, Calif., April 17, 1947 (Beck 4450), adult male, Missot, BC, May 2, 1920 (AB 1284), and adult male, Osoyoos, BC, May 7, 1922 (AB 1291).



PLATE 6

Winter plumage of *L. guscus*, shown in ventral view. Specimens, left to right: first year male, Amelia I, Fla., November 17, 1905 (CM 133832), adult female, La Paz, Baja Calif., December 14, 1933 (CM 158024), first year male, Puerto El Triunfo, El Salvador, January 16, 1926 (CM 111238); adult female, National City, Calif., October 20, 1917 (CM 133825), adult male, Piedra de Blanca, Costa Rica, February 8, 1924 (CM 74642); adult male, Pt. Jimenez, Costa Rica, December 5, 1929 (CM 157984).



PLATE 7

Winter plumages of *L. scolopaceus* (specimens 1-4, bottom to top) and *L. griseus* (specimens 5-6). Specimens, bottom to top: first year male, Merced, Calif., March 23, 1945 (C'AS 60915); adult female, Merced, Calif., October 20, 1943 (MVZ 96928); adult female, Merced, Calif., November 20, 1946 (MVZ 97079); adult male, Merced, February 12, 1945 (MVZ 94361); adult female, Alimtos Bay, Calif., December 15, 1930 (C'M 158010); adult female, same place and date as last (C'M 160547).



PLATE 8

Juvenal plumages of *Limnodromus scolopaceus* (four lower specimens) and *L. griseus* (three upper specimens), shown in dorsal view. Specimens, bottom to top: female, Okanagan, B.C., September 20, 1932 (AB 5628); male, Okanagan, B.C., October 2, 1936 (AB 8385); male, Canoe Pass, B.C., September 1, 1941 (KR 2770); female, Merced County, Calif., September 28, 1908 (CAS 12529); male, Comox, Vancouver I., B.C., August 17, 1931 (AB 7749); female, Santa Barbara, Calif., August 22, 1911 (JEL 1420); male?, Crescent Beach, Nova Scotia, August 28, 1925 (AB 1278).



PLATE 9

Juvenil plumages of *Timnodromus scolopaceus* and *T. griseus*. Same specimens as in plate 8. Shown in ventral view. The marked gray coloration of two specimens at the top actually indicates marked buffness which was registered in photographing by use of a green filter.

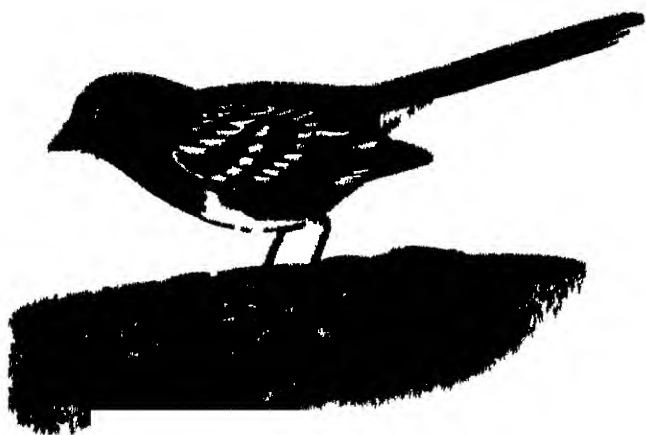
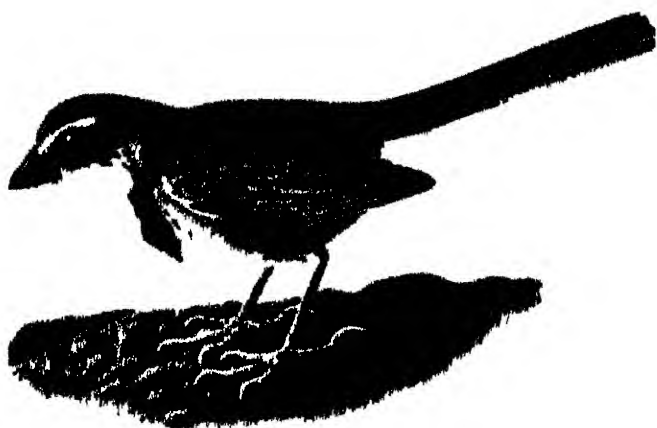


PLATE 10

a Downy young of *Limnodromus griseus hendersoni* (four specimens to left) and *L. scolopaceus* (four specimens to right) shown in dorsal view. Specimens left to right: Pawcett, Alta., July 19, 1914 (HBC 1140, 11407, 11408); Churchill, Man., June 21, 1917 (HBC 1562); Collinson Pt., Alaska, July 20, 1915 (CM 160545); Yukon Delta, Alaska (NMC 22,10); Collinson Pt., Alaska, July 20, 1915 (CM 157965, 160544).

b *Limnodromus griseus griseus* adult female, Marshfield, Mass., May 25, 1913 (MCZ 157852).





♂, SIBBINS

Typical examples of the two species of red eyed towhees of Mexico Upper *Pipilo ocai*
guerreroensis Lower, *Pipilo erythrophthalmus orientalis*

SPECIES FORMATION IN THE RED-EYED TOWHEES OF MEXICO

BY
CHARLES G SIBLEY

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SPECIES FORMATION IN THE RED-EYED TOWHEES OF MEXICO

BY

CHARLES G. SIBLEY

(A contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

THE NEO-DARWINIAN contention that species are gradually formed from pre-existing species by the accumulation of differences in isolated populations through the fixation of micromutations is supported by a growing mass of evidence. Some of the most conclusive evidence supporting microevolution is that relating to the results of secondary contacts between two populations which have attained partial or complete physiological isolation although they have but recently diverged from one another. Such secondary contacts are the proving grounds for testing the degree of isolation which has been attained in the dynamic process of species formation. If complete physiological isolation has been attained, the two forms will live as sympatric species and continue to diverge although existing side by side. If the degree of separation attained by the time the secondary junction is established is not sufficient to maintain isolation, the result will be hybridization.

The amount of hybridization and the degree of fertility are proportional to the degree of isolation which has been reached. If sympatric occupation of an area by two closely related forms signifies completion of species formation, a small amount of hybridization is indicative of the near completion of isolation, and so on to the point where the secondary contact results in the complete swamping out of any differences. Thus there is theoretically a complete graded series of possible degrees of response from the pattern of free interbreeding between subspecies, through all degrees of hybridization and interfertility, culminating in sympatric species. If the neo-Darwinian theory of microevolution is correct, we should find examples in nature of these varying degrees of hybridization.

The red-eyed towhees, *Pipilo erythrophthalmus* and *Pipilo ocai*, of the central Mexican highlands have presented difficult problems to avian systematists ever since their discovery more than a century ago. The difficulties have arisen from the differing interpretations placed upon specimens that were morphologically intermediate between "good" species. Any success in solving the problems in the present study is due primarily to firsthand knowledge of the complex topographical and ecological situations along with extensive collecting at critical localities.

The analysis of the results of four secondary contacts between *P. erythrophthalmus* and *P. ocai* constitutes the principal contribution of this paper. A systematic revision of the Mexican red-eyed towhees is presented, as well as some information on ecology and natural history.

MATERIALS

Two field trips to Mexico were made for the purpose of collecting material. The first, between June 22 and August 7, 1946, was to survey the problem areas and to visit the type localities. Collections of towhees were made at ten localities in the states of Hidalgo, Puebla, Oaxaca, México, Guerrero, Michoacán, and Jalisco. The second expedition was made from February 16 to April 26, 1948. Towhees were taken at twelve localities in the states of Nuevo León, San Luis Potosí, Puebla, Oaxaca, Chiapas, Michoacán, and Jalisco. Special attention was given to the series of populations extending across the plateau from México to Jalisco: the hybrid population of Cerro Viejo, Jalisco; the hybrid zone on the western slope of Mount Orizaba, Puebla; and the sympatric populations of Cerro San Felipe, Oaxaca.

Additional material was obtained on loan from the following: United States Biological Survey, through Dr. John W. Aldrich; United States National Museum, through Dr. Herbert Friedmann; American Museum of Natural History, through Dr. J. T. Zimmer; Museum of Comparative Zoölogy, through Mr. J. L. Peters; Chicago Natural History Museum, through Mr. E. R. Blake; University of Michigan, through Dr. J. Van Tyne; Cornell University, through Mr. Dwain W. Warner; Louisiana State University, through Mr. George H. Lowery, Jr.; Los Angeles Museum of History, Science, and Art, through Mr. Kenneth W. Stager; Carnegie Museum, Pittsburgh, through Mr. W. E. C. Todd and the Sutton Collection, through Dr. George M. Sutton.

The collections of the California Academy of Sciences (courtesy of Dr. Robert T. Orr) and those of the University of Kansas, Museum of Natural History (courtesy of Dr. E. Raymond Hall), were examined.

The specimens examined in connection with this paper total somewhat more than 1,156. Of these, 927 were used in critical comparisons; 779 were from Mexico.

ACKNOWLEDGMENTS

Besides the aid given by the persons mentioned in the list of those who have loaned specimens, or who made available the collections under their care, I gratefully acknowledge the following assistance: Mr. John Davis, my field companion in 1946, collected many critical specimens and examined others in the collections of the American Museum of Natural History in my behalf. My companions in 1948, James Basil Bowers and Henry Everett Childs, Jr., made possible the accumulation of large series from critical localities in the short time available for each locality. Dr. A. J. van Rossem kindly permitted me to examine his notes on the types of *Pipilo macronyx* and *P. ocai*. Dr. R. Stohler checked the German translations, and Dr. Arthur E. Gordon aided in the translation of Latin passages. Without the kindness of Señor Agustín Perez Gomez of Guadalajara, Jalisco, the ascent of Cerro Viejo would have been far more difficult. I have had the advantage of guidance, in the study

of the material and preparation of the manuscript, from Dr. Alden H. Miller and Dr. Frank A. Pitelka. Dr. G. Ledyard Stebbins, Jr., read the manuscript and made several helpful suggestions concerning genetic interpretations. Frances L. Sibley made most of the measurements and computed the statistics, Lois C. Taylor made the maps and graphs, and Dr. Robert C. Stebbins made the colored illustrations.

DESCRIPTIONS OF SPECIES

In the following pages, numerous references will be made to characters of plumage color and pattern in *Pipilo erythrophthalmus* and *P. ocai*. The following descriptions will serve to point out the differences and similarities between them. These descriptions are of "normal" representatives of each species, such as *P. e. orientalis* and *P. o. guerrerensis*. The frontispiece (pl. 11) was drawn from the type of *P. e. orientalis* and from a typical specimen of *P. o. guerrerensis*. The descriptions follow Ridgway (1901:406 and 410), but are somewhat modified.

Pipilo erythrophthalmus (spotted races). Head, neck, and chest black; upper parts black with white spots on scapulars and interscapulars; middle and greater wing coverts tipped with white, forming two bands; bend of wing white; the three or four outer tail feathers with large terminal spots of white, chiefly on inner webs, these spots averaging about 30 mm. long on outer rectrix; breast and abdomen white; sides and flanks rufous or cinnamon buff; crissum and under tail coverts paler than flanks; iris red; bill black; legs and feet pale horn color.

Sexual differences are only in depth of color of the black areas, the female being dull or sooty black rather than deep black.

Pipilo ocai. Forehead black, with narrow median frontal line of white; rest of pileum cinnamon rufous or chestnut, margined laterally with narrow line of black; broad superciliary stripe, malar region, chin, throat, and median underparts white; sides of head and broad, sharply defined pectoral collar black; upper parts (except head) uniform olive green, including wing coverts; bend of wing bright yellow; sides grayish, becoming more olive on flanks; under tail coverts buffy; iris reddish brown; bill black; legs and feet pale horn color.

The sexes are alike.

METHODS OF ANALYZING CHARACTERS

Color comparisons between populations were made in the usual manner, that is, between series of specimens of comparable age, sex, and plumage condition. Such comparisons were ordinarily made between adult males in unworn, or but slightly worn, plumage. The age of compared specimens was determined by the method described on page 114. This type of simple comparison serves adequately for delineation of differences or similarities between normally variable populations, but it was found to be inadequate to cope with the extreme variation found in the hybrid populations encountered. Therefore a special method was devised.

Because hybrids are the result of crossing between two unlike parents, it is usually possible to determine the source of a given character in the hybrid

individual. This is true in hybrids formed between *P. ocai* and *P. erythrophthalmus*. *P. ocai* and *P. erythrophthalmus* differ in six primary characters:

1. Pileum color: Chestnut in *ocai*, black in *erythrophthalmus*.
2. Back and wing spots: Scapulars and wing coverts spotted with white (or yellow) in *erythrophthalmus*. These areas are a solid color (green) in *ocai*.
3. Back color: Green in *ocai*, black in *erythrophthalmus*.
4. Throat color: White in *ocai*, black in *erythrophthalmus*.
5. Flank color: Brownish or grayish olive in *ocai*, rufous in *erythrophthalmus*.
6. Tail spots: White spots present on three (usually) outer rectrices of *erythrophthalmus*, absent in *ocai*.

Other differences between the two forms are correlated with some one of the six primary characters. For example, when the amount of black in the head region of *ocai* increases, the white throat is restricted and the white superciliary and median frontal lines become clouded with black or eliminated. Thus the condition of the throat is actually an index to total blackness of the head. No significant correlation in expression of any two of the six primary characters has been noted, although back spotting and tail spotting tend to occur together. This may be seen by comparing these two characters in the graphic analysis of individuals in figure 13.

Hybrids between *ocai* and *erythrophthalmus* possess the six (or twelve) primary characters in varying amounts. Therefore, not only is it necessary to analyze mere presence or absence, but some index to relative amount of the character must also be obtained. By separating the Cerro Viejo hybrids into groups based upon the six primary characters in turn, it was found that not more than five gradations could be discerned in any one character. Thus, for pileum color, individuals with as much chestnut as pure *ocai* and, at the other extreme, those with pileums completely black, as in pure *erythrophthalmus*, formed the two terminal groups. Between these, three gradations from one pure extreme to the other could be separated. Finer units were not found to be practical. A scale of 0-4 was adopted to indicate quantitatively the amount of each of the primary characters visible in each specimen. A pure *ocai* was considered to be at the "0" end and a pure *erythrophthalmus* at the "4" end of the scale. Thus a character expressed in an exactly intermediate amount between the pure extremes would rate a score of "2"; one between the pure *ocai* type and an intermediate, or "2," specimen, would rate 1; one between the midpoint at "2" and a pure *erythrophthalmus* would rate a score of "3." Since there are six characters with a quantitative spread of five units (0-4) each, any individual of any race of pure *P. ocai* will add up to "0," and any individual of any race of pure *P. erythrophthalmus* will add up to 24 ($= 6 \times 4$). The summation of the characters of a hybrid specimen may be expressed in terms of one number on a scale from 0 to 24. Thus a specimen with a score of "12" will be a perfect intermediate between *ocai* and *erythrophthalmus*.

Table 1 describes the gradations of each character. These descriptions were made from the observed gradations. They do not represent a scale of standards set up beforehand into which specimens were fitted.

TABLE 1
SYNOPTIC DESCRIPTIONS OF QUANTITATIVE UNITS USED IN COLOR ANALYSIS
OF HYBRIDS BETWEEN *Pipilo ocai* AND *Pipilo erythrophthalmus*

FILEUM

- 0=as much chestnut as in *P. ocai*
- 1=black tips or reduced size of chestnut patch
- 2=one-half size of *P. ocai* crown patch or with considerable admixed black
- 3=chestnut tips and (or) shaft streaks to basically black crown feathers
- 4=as in *P. erythrophthalmus*; solid black

BACK SPOTS

- 0=as in *P. ocai*, no spots or indication thereof
- 1=faintly defined light area on coverts, nothing on scapulars
- 2=well-defined spots on coverts plus some edgings on scapulars
- 3=many scapular spots; fully spotted coverts
- 4=as much as in spotted races of *P. erythrophthalmus*

BACK COLOR

- 0=solid green as in *P. ocai*, no shaft streaks
- 1=solid green as in *P. ocai*, but with shaft streaks
- 2=green, but with wide black bars along shafts
- 3=green faded, black dominant
- 4= as in *P. erythrophthalmus*

THROAT

- 0=collar as in *P. ocai*, solid white throat
- 1=broad white throat patch, reduced from *P. ocai* type
- 2=narrow bar down center of throat; may have malar stripes also white
- 3=small amount of white visible, but mostly black
- 4=solid black, no visible white

FLANKS

- 0=brown or gray as in *P. ocai*, no rufous
- 1=brown or gray with some traces of rufous
- 2=mixed brown and rufous
- 3=rufous with brownish tipping or suffusion, rufous dominant
- 4=as in *P. erythrophthalmus*, entirely rufous

TAIL SPOTS

- 0=no trace of white, as in *P. ocai*
- 1=white tips visible, usually 1-2 mm. broad
- 2=well-defined white spots, up to 5 mm.
- 3=large white spots (may be clouded), 5-10 mm. long
- 4=as in *P. erythrophthalmus*

Linear dimensions from skins, in millimeters, were taken as follows: wing, the chord; tail, from insertion of the two middle rectrices; bill length, from anterior margin of nostril to tip; tarsal length, from joint between tibiotarsus and tarsometatarsus to the midpoint of the distal margin of the lowest undivided scute; and hind toe plus claw, from the palmar fold on the ventral side to the tip of the claw. Depth of bill, measured from the culmen across the anterior margin of the nostrils to the ramal junction, was taken for some populations.

DETERMINATION OF AGE

In order to be certain that specimens used in making racial comparisons were of comparable age and in comparable plumages, it was necessary to investigate the problem of molts and plumages. Dwight (1900:206-207) found that in *P. erythrophthalmus* the first winter plumage is acquired by a partial post-juvenal molt in which all feathers but the primaries, secondaries, and primary coverts are replaced. These unreplaced series are retained from the juvenal plumage and are not molted until a year later, when the entire plumage is replaced in the first postnuptial molt. A bird hatched in May of one year will therefore carry its juvenal primaries, secondaries, and primary coverts for about the first fifteen months of its life. Because the juvenal feathers are browner than those acquired in the first winter, those birds in the first year of life may be determined by the contrast between the primary coverts and the secondary coverts, which in the males will be black. In females the contrast is not great enough to permit dependable age determination.

In order to test the accuracy of determining age by the contrast between primary and secondary coverts, a series of 19 fall-taken males, marked adult or immature on the basis of skull ossification, was assembled. Of these, 13 were marked immature. All 13 have brown primary coverts contrasting with black secondary coverts: 4 marked adult have both primary and secondary coverts black, showing no contrast; 2 marked adult have brown primary coverts, but are August birds in excessively worn plumage, indicating that they are birds about one year old, hence with fully ossified skulls, but which have not yet passed through the first postnuptial molt. The correlation between skull and plumage is thus 100 per cent in these 19 birds.

Another group of 8 male specimens from San Luis Obispo and Kern counties, California, taken in September, 1947, presents further problems. These birds were aged by skull ossification and were determined by completely reliable collectors. Of these, 5 were marked immature and 3 adult. The 3 adult birds show the expected black primary coverts, and 3 of those marked immature have brown primary coverts. The other 2 birds marked immature, however, have black primary coverts and appear to be in fully adult plumage. If we assume that these 2 birds are correctly aged, the characters just described may indicate that some individuals go through a complete molt when only four or five months old, and hence take on fully adult plumage in their first winter. The evidence is too meager to permit any conclusions, but it suggests that there may be a situation in the towhees similar to that described in *Phainopepla* by Miller (1933:435-440) wherein some immature birds showed much blacker plumage than others. It may be that birds hatched in the early part of the season have become sufficiently matured by the time of the postjuvenal molt to undergo a complete replacement. Thus, although it may safely be assumed that all males showing brown primary coverts in contrast to black secondary coverts are immature, there is not complete certainty

that all birds with black primary coverts are more than one year old. For purposes of comparison they may all be considered adult since the crypto-immatures cannot be detected and the plumage characters are those of adults.

All critical comparisons of both color and size in the present study were made between specimens of comparable age as determined by the color of the primary coverts, unless otherwise noted. For the most part, only adult males were used. Age determination by this method is possible in the races with

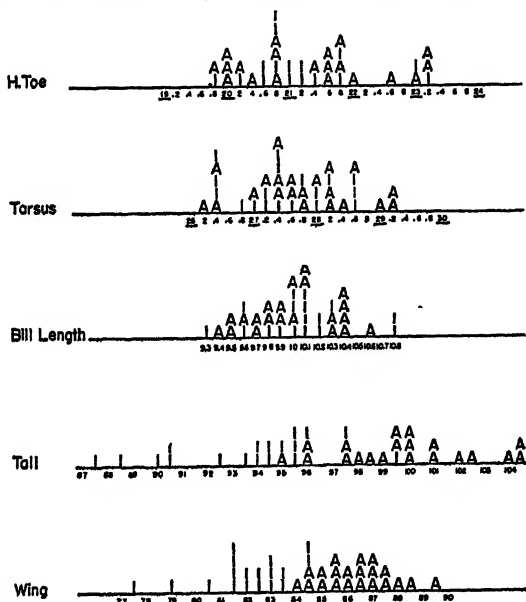


Fig. 1. Age groups compared with measurements in *Pipilo erythrophthalmus*. A, indicates adult individual; I, immature. Curves for wing and tail are markedly bimodal, but measurements for bill, tarsus, and hind toe show no significant differences between adults and immatures. Histogram based on males from populations of *P. e. orientalis* of the Sierra Madre Oriental.

black dorsal coloration well developed, as in *montanus*, *gaigei*, *griseipygius*, *orientalis*, *maculatus*, *oaxacae*, *chiapensis*, and *repetens*. In the greener races (*vulcanorum* and *macronyx*), however, it was impossible to make a satisfactory distinction. In these races comparisons were made between the most intensely colored males in each population, on the assumption that these are the most adult individuals.

Immature birds have shorter wings and tails than adult birds. This is proved by comparing the two age groups, determined by the primary covert method. The histogram (fig. 1) shows the markedly bimodal curve obtained for wing and tail measurements when the two age groups are plotted. Bill, tarsal, and toe measurements give no indication of significant differences between adults and immatures.

A completely satisfactory method for separating first-year birds from adults in *P. ocai* was not found. It was discovered that the birds of the year could be separated until about December by the light-brown edgings to the innermost secondaries. The juvenal plumage in *P. ocai* has these edges well developed, but by January they are worn off and immature birds can no longer be detected. Using the method described above, fall birds of the Guerrero population (*P. o. guerrenderensis*) were separated and analyzed separately. The results of this analysis are presented in table 12. In all the characters measured except hind toe, the immatures are seen to be smaller than the mixed sample containing adults and undetectable spring immatures.

NOMENCLATURAL PROBLEMS

The application of several names in the present paper is at variance with current nomenclature. Two principal problems of name change arise. The first involves the evidence in support of merging the spotted and unspotted groups (*maculatus* and *erythrophthalmus*) in one species. The second is evidence supporting a change in the application of the name *macronyx*.

THE ERYTHROPTHALMUS-MACULATUS PROBLEM

The traditional allocation of spotted and red-eyed towhees to different species has been based on the following factors:

1. The presence or absence of white spots on the scapulars, interscapulars, and wing coverts.
2. The degree of sexual dimorphism.
3. Differences in song and call notes.
4. Lack of actual contact between the two groups and hence lack of intergradation.

Examinations of the synonymies of the two groups will reveal that some authors have in the past united them in one species (see Ridgway, 1901:413-423). Hellmayr (1938:461) was not willing to break with tradition when he wrote, "I follow general custom in keeping the Red-eyed Towhee as specifically distinct from *P. maculatus*, though I feel almost certain that their proper relationship would be more correctly expressed by uniting them in one complex." It is apparent that doubt in regard to the specific status of the two forms has plagued others in the past.

It would seem at first glance that the presence or absence of white spots on back and wings would offer a fairly sharp line of division. The truth is that many specimens of otherwise typical *P. e. erythrophthalmus* have varying amounts of white spotting on the same feathers which are normally spotted in the races inhabiting Mexico and the western United States. The occurrence of white dorsal spotting in *P. e. erythrophthalmus* was first placed on record by Baird, Cassin, and Lawrence (1860:513). They noted a specimen from Leavenworth, Kansas, which had white spots in the scapulars, and indicated that they suspected it to be the result of crossing between *erythrophthalmus* and *arcticus*.

Coues (1874:174) noted that specimens of *P. erythrophthalmus* "... from the Red River region show an interesting approach to var. *arcticus* in the presence of small, concealed white spots. It may be necessary, after all, to bring the species into the same series with *maculatus*, and consider all the forms as varieties of one species." The same author (1874:175-176) wrote as follows under *P. maculatus*:

The connection of the several spotted *Pipilos* of the west and of Mexico, I believe first noted by Dr. Sclater, has been amply confirmed by subsequent investigation. They unquestionably intergrade completely, forming geographical races of one species. The question is, whether to this series *P. erythrophthalmus* should not also be added. In the Key, I kept it apart and presented the considerations favoring this view, viz., the entire absence of spotting on the scapulars and back, the stronger sexual distinctions, and the different note—the cry of the western species resembling that of the Cat-bird. It would not, however, be at all surprising if complete intergradation between *erythrophthalmus* and *arcticus* were proven by specimens from the Lower Missouri, gaining first a spot or two, and then gradually assuming the fully speckled state. In that event, I should not hesitate to combine the whole in one series, beginning with the black unspotted *erythrophthalmus*, with clear brown female, and ending with the olive-shaded, spotted *maculatus* and its nearly similar female. Dr. Hayden has shown exactly where the two forms meet along the Missouri, at about 43 degrees. In Northern Dakota var. *arcticus* occurs east to about 102 degrees longitude, and my Red River specimens of *erythrophthalmus* show an approach toward it.

A few years later Coues (1878:41) published the following description of an eastern towhee shot on May 4, 1875, in Washington, D.C., by P. L. Jouy.

The outer scapulars are distinctly and strongly marked, near the end of the outer webs, with streaks of pure white; there is much concealed white in the black of the throat; and in other respects, as the extent of white in primaries and lateral tail-feathers, the specimen resembles *P. arcticus*. Nothing is wanting, in fact, to make it a typical *arcticus* but the spots on the wing-coverts. Another specimen, shot by the same gentleman in the same locality, also shows a trace of white on the scapulars. Examples intermediate between *erythrophthalmus* and *arcticus* have long since been noted... but all such hitherto known, so far as I am aware, have been from localities where the respective *habitats* of the two forms adjoin. The present case offers additional and very strong evidence against the specific distinction claimed for *P. arcticus*.

To this article of Coues, J. A. Allen added an editor's note as follows:

A considerable proportion of the specimens of *P. erythrophthalmus* taken by me in 1871, in the vicinity of Leavenworth, Kan. (mainly in East Leavenworth, Mo.), showed white spots on the scapulars and more white on the wings than eastern examples, thus exhibiting a decided tendency toward the characters of *P. arcticus*, the eastern limit of the range of which, in its typical aspect, is the eastern base of the Rocky Mountains in Colorado, some six hundred miles west of Leavenworth.

Baird, Brewer, and Ridgway (1874:516) commented upon specimens, which were probably the same birds mentioned above by Coues, as follows:

Specimens collected by Dr. Coues at Pembina, Minnesota, in June, 1873, have (both males and females) a greater or less number of minute white specks more or less distinctly indicated on the portion where the large white spots of the western forms are located. This points to the probability that all the black races ranged in the synopsis under *maculatus* (including the latter itself) must be referred to as *erythrophthalmus*.

Goss (1891:482) wrote, "I find occasionally in Kansas signs of intergradation with *P. erythrophthalmus*; that is, specimens with a few white wing spots, and others grading up to the fully speckled state." Miller (1897:276) recorded a spotted eastern towhee taken at North Truro, Massachusetts, on August 12, 1889, which was "... normal in all respects except that the scapulars on each side are conspicuously edged with white. The marking is only slightly less extensive than in a specimen of *Pipilo maculatus oregonus* taken at Victoria, B.C., on August 1, 1888. Eastern towhees with spotted scapulars have been recorded before but such specimens are always of interest." Taverner (1927:226) recorded a specimen under *P. maculatus* from Whitewater Lake, Manitoba, taken on May 4, 1925, with the note that "It is clearly of this species, though in the amount of white on the sides of the back and on wing coverts, it is not quite typical. This is the first record for the species in Manitoba." Whitewater Lake is only 20 miles north of the Turtle Mountains from which Judd (1917:24) recorded *P. erythrophthalmus* as "Rare. May be found breeding. . . ."

Since becoming aware of the existence of the specimens described above, I have examined all possible specimens of *P. erythrophthalmus* in a search for more individuals with dorsal spotting. Although no special loans or trips were made, it was possible to find 18 more specimens from localities in the eastern United States and Canada with small amounts of white on the scapulars. These specimens are listed below.

California Academy of Sciences. Total of 47 *Pipilo erythrophthalmus*

- No. 23113. Male. West Roxbury, Mass. May 21, 1898
- No. 52209. Male. Near Savannah, Georgia. Nov. 20, 1906
- No. 52210. Male. Milton, Wisconsin. April 4, 1894
- No. 52214. Male. Mandeville, Louisiana. April 11, 1904
- No. 52221. Female. London, Ontario. April 10, 1899

University of Kansas, Museum of Natural History. Total of 82 *P. erythrophthalmus*

- No. 970. Male. Lawrence, Douglas Co., Kansas. March 3, 1906
- No. 8696. Male. 3 mi. E Concordia, Cloud Co., Kansas. Oct. 14, 1911
- No. 22087. Male. 4 mi. SE Columbus, Cherokee Co., Kansas. June 16, 1937
- No. 22722. Male. Fort Leavenworth, Leavenworth Co., Kansas. July 10, 1939

Los Angeles County Museum. Total of about 100 specimens

- No. 9807. Male. Augusta, Wisconsin. June 25, 1894
- No. 9809. Male. Berwyn, Cook Co., Illinois. April 28, 1906

American Museum of Natural History. (Only males examined)

- No. 41648. Male. Long Island, New York
- No. 84177. Male. Erie, Pennsylvania
- No. 114083. Male. Rockaway, Long Island, N.Y.
- No. 367948. Male. Cresson, Pennsylvania
- No. 367988. Male. Jamaica, Long Island, N.Y.
- No. 368051. Male. Broadrun, Virginia
- No. 441728. Male. Montauk, Long Island, N.Y.

I am confident that examination of any series of 50 or more *P. e. erythrophthalmus* will reveal additional specimens with the narrow edgings, or small spots of white on one or more scapulars, which these listed specimens possess.

Differing degrees of sexual dimorphism constitute good racial characters, but unless they are accompanied by unassailable evidence of specific value, they can hardly be considered a valid basis for the separation of species. Within the spotted races there is considerable variation in the degree of sexual dimorphism. The race *arcticus*, for example, is more marked in this regard than the west-coast forms. Intraspecific geographic variation in the degree of sexual dimorphism has been summarized by Mayr (1942:48-50), who cites several examples more extreme than the differences between eastern and spotted towhees.

The songs and calls of typical *P. e. erythrophthalmus* and the races of the western United States are quite distinct. It is necessary only to compare the Florida race *P. e. alleni* and the Mexican races, for example *P. e. orientalis*, in order to break down completely any real or fancied differences in either song or call notes. Peterson (1947:22) syllabifies the song of *P. e. alleni* as "cheet cheet cheeeeee." This is the song often heard from Mexican birds, and even some of the western races, for example *curtatus*, have a very similar song. I have heard *P. e. orientalis* sing a song very close to the "drink-your-tea" of *P. e. erythrophthalmus* which I described as "chip-cher-cheee."

The call note of *P. e. alleni* is recorded by Peterson (1947:22) as "shrink" or "zreee." All Mexican races call "zreee" and the mewing call of western United States forms is not far from it. Howell (1932:449) records the call of *P. e. alleni* as "a single short zree." This is precisely how I have repeatedly described the call of the Mexican races in my field notes.

The strictly allopatric distributional pattern of the eastern and western races argues strongly for, rather than against, their being considered conspecific. The evidence presented in the foregoing paragraphs on back spotting strongly suggests that intergradation does take place. The probable site of actual intergradation is in southwestern Manitoba, where the two forms have been recorded within 20 miles of one another.

Besides the evidence presented above, several other facts argue for conspecificity:

1. In all plumage characters other than dorsal spotting, the two are identical except for normal geographic variation.
2. Eggs and nests are no more different than is to be expected between subspecies.
3. Ecological requirements vary more within the spotted races than between the spotted and eastern ones
4. Since the extremely different-appearing *P. ocai* interbreeds with the spotted group in Mexico, it is hardly likely that the very similar North American forms would not interbreed if they came into contact.

The differences are thus seen to be of no more than subspecific value. Not one of the alleged specific differences holds constant; on the contrary, all are shown to break down at some point. I therefore advocate the merging of the *maculatus* and *erythrophthalmus* groups of the genus. Since *erythrophthalmus* has many years of priority over *maculatus*, it becomes the species name.

The "species" *macronyx* is also herein included in *erythrophthalmus* because it too is merely a subspecific unit within that species. The reasons for this action are fully explained on pages 120-125.

THE MACRONYX PROBLEM

In 1827 Swainson described two new "species" of the genus *Pipilo* from Mexico. Both were founded on specimens brought back to England by William Bullock. These two birds were characterized as follows (1827:434):

44. *Pipilo macronyx*. Olive, head and throat black, body white, sides and vent ferruginous; wings and lateral tail feathers (in one sex) with yellow spots. Table land, Real del Monte, Temiscaltepec. Total length, 9 inches; wings, $3\frac{1}{2}$; tail, $4\frac{3}{4}$; tarsi, $1\frac{1}{10}$; hind toe and claw, $\frac{9}{10}$.

45. *Pipilo maculata*. Olivaceous brown; head and throat black; body white; sides and vent rufous; back, wings, and lateral tail feathers with white spots. Table land; Real del Monte. Total length, $8\frac{1}{2}$; wings, $3\frac{1}{2}$; tail, 4; tarsi, $1\frac{1}{10}$; hind toe and claw, $\frac{3}{4}$.

The following points concerning these descriptions are of significance: (1) *P. macronyx* is described as having yellow spots; *maculata* as white-spotted. (2) *P. macronyx* is recorded from Real del Monte, Hidalgo, and Temascaltepec, México. *P. maculata* is recorded only from Real del Monte. (3) The size of *P. macronyx* (total length and tail, especially) is greater than that of *P. maculata*.

Eleven years later, Swainson (1838:347) presented another description of "*Pipilo macronyx*." Again the yellow spots contrasted with the white ones of *maculata* are stressed. The measurements given in 1827 do not agree with those of 1838, except those of the hind toe. I attach no particular significance to this. Probably it merely indicates that the type was remeasured and different numbers obtained. It does point up the fact that no great significance should be attached to the measurements made by Swainson. Swainson here more specifically mentions a second specimen, which he believed to be the female, as having "no yellow spots whatever." This specimen is noted as differing from the spotted one only by the absence of the spots.

The next paper which has bearing on this problem was Hartlaub's (1863:228) description of *Pipilo virescens*. A translation of Hartlaub's Latin and German text follows:

Above olivaceous brown, head and neck becoming blacker; back feathers medially darker lengthwise; nape somewhat ashy; wings doubly banded with yellow with apical spots on coverts; external edges of wings and tail remiges and rectrices brighter green; throat dark blackish; abdomen white; sides, crissum, and under tail region (= coverts) bright rufous; two rectrices on each side marked with a half-thumb-sized spot on inner vane; bill black; feet pale.

Of this typical species of *Pipilo* we have seen two identically colored examples. Both were obtained in Mexico by Prince Maximilian of Wied, and one is now in the Bremen Collection. A confusion with one of the described species is scarcely possible. *Pipilo arcticus* is considerably smaller and differs, aside from other color differences, principally also by the fact that in this [species] the four outer tail feathers on each side show a small white spot at the tip on the inner vane, which on the outermost one is a full inch long. On the other hand, in

Pipilo virescens only the two outer rectrices on each side have an end spot about six lines long. *Pipilo arcticus* shows no trace of green in the plumage, which is the dominant color of the wings and tail of *Pipilo virescens*. I was able to compare the new, to me unknown, Mexican form with *Pipilo erythrophthalmus* ♂ and ♀, *arcticus* ♂ ♀, *maculatus*, *fuscus* (*crissalis*), *albigularis*, *chlorurus* and *megalonyx*, all in the Bremen Collection.

[The Berlin Museum possesses several specimens in different plumages of the species discussed above. The adult birds were named *Tanagra melanops* and the younger, in subadult plumage, *Fringilla scutata* by Lichtenstein. Both unpublished names I later believed to be synonymous with *Pipilo macronyx* Sws. since the birds seemed to me to belong to this one of the forgotten Swainsonian species. Dr. Hartlaub's excellent description will be a welcome contribution in the final clarification of the question.—THE EDITOR.]

The significant points in the description of *Pipilo virescens* are:

1. The species is described as having only the two outer rectrices spotted, and the spots are "about six lines long." Six lines = $\frac{1}{2}$ inch. This description can fit only the population of the western side of the Valley of Mexico.
2. Green is noted as the "dominant color of the wings and tail."
3. All other characters could be matched in either the population of Mount Popocatepetl or in that of the western side of the Valley of Mexico.

The description is sufficiently detailed to permit positive identification of *Pipilo virescens* with the population to which it has long been applied, namely, that of the western side of the Valley of Mexico (Volcán de Toluca).

The next published description of the type of *Pipilo macronyx* was that of Salvin and Godman (1904:406).

Above dark greenish; wings and tail bordered with olivaceous; [its] three outer rectrices on both sides near the ends and externally greenish white on the outer vanes, all the coverts tipped with greenish white; head dark blackish, interscapular region streaked with blackish (or dusky), feathers (of the interscapular region) also spotted laterally with greenish white; below white, flanks and crissum chestnut; bends of the wings yellow; bill black; feet pale. [Translation of Latin.]

Of this species we have Swainson's two types before us, and four other specimens from Southern Mexico, including one sent to Mr. Selater by Dr. Hartlaub as a type of *Pipilo virescens*. These present very considerable differences in coloration, which have doubtless given rise to the many names bestowed upon the variations in plumage. The bird described by Swainson has very distinct yellowish-white spots on the wing-coverts and scapulars, and the sides of the interscapulum are similarly spotted. In *Pipilo virescens* these spots are present on the wing-coverts, but absent from the interscapulum. In *Pipilo chlorosoma* they are said to be absent altogether, as they are in one of Swainson's types and in another example in our collection. *Pipilo complexus* is said to have a white spot on the throat and a rufous patch on the head. A specimen from Southern Mexico (Boucard) has the white spot very distinctly shown, and also white on the chin and white lores; it has also some rufous on the occiput. Another example has more rufous on the occiput, but not so much white on the throat; both have obvious characters of immaturity, and we have little doubt that Mr. Ridgway's name was founded on an immature specimen of *Pipilo macronyx*. Another variable point is in the spots of the outer rectrices—in some (as in the type) the outermost exceeds an inch + in length, in others they are quite evanescent, presenting a mere trace; so too with the length of the tail, which varies from 4.8 inches (type) to 4.3 inches.

Nothing has been recorded concerning this species in Mexico; but we find on a label attached to one of Swainson's types the following note, doubtless written by Bullock:—"I have never seen this bird anywhere but between Mexico and San Miguel, nor is it found

within five leagues of the capital. It is extremely tame and constantly in motion, and hides itself in thick bushes. Eye deep red and very small."

Of significance in this paper are these facts :

1. The description is from Swainson's type.
2. The variations in spotting described for *macronyx*, *virescens*, and *chlorosoma* are all present in the single freely interbreeding population of the western side of the Valley of Mexico. (*P. complexus* is a hybrid between *P. e. maculatus* and *P. o. ocai*.)
3. Of especial significance is the note attached to the type (*vide* van Rossem MS, 1938) which is quoted in full on pages 121-122. The San Miguel referred to is fully identified and located by Bullock himself (1824:432), who wrote as follows: "On going to and returning from Temascaltepec [*sic*], I have passed four nights in the Indian town of St. Miguel de las [*sic*] Ranchos . . . which is about eighteen miles from Temascaltepec . . ." On pages 347-348, in describing his first trip to Temascaltepec in which the route lay from the city of Toluca via San Miguel de los Ranchos, Bullock writes: "We left Toluca [*sic*] in the coach, and proceeded about two leagues . . . where the road for wheel-carriages ceases. Here having procured horses . . . we ascended about a league, and then entered an extensive wood, which crowned the Cordillera, on the west side of the Table-land of Mexico . . . and in one elevated open place caught the last view of the mountains that surround the vale of Mexico: on our left lay the volcano of Toluca, covered with perpetual snow; and shortly after we reached a defile in the mountain, and began to descend toward the Pacific ocean."

The position of San Miguel is thus accurately fixed as the western side of the Volcán de Toluca (because the Volcán de Toluca was on Bullock's left as he went south), 18 miles from (= NE of) Temascaltepec. The *Atlas Geográfico da la República Mexicana* (Dirección de Geografía, Meteorología e Hidrología, Tacubaya, D.F., 1943, Hoja *México*, no. 26) shows a "S. Miguel" 20 km., in an air line, northeast of Temascaltepec. This places it on the western shoulder of the Volcán de Toluca. Bullock's journey to San Miguel took him from Mexico City via Tacubaya (1824:344), Lerma (p. 345), and Toluca (p. 346), hence he was entirely within the limits of the towhee population to which Hartlaub's name *virescens* is currently applied.

No further description of the type of *Pipilo macronyx* was written until 1938, when Dr. A. J. van Rossem visited the Cambridge Collection and prepared the following notes from the type :

Pipilo macronyx Swainson | Type | No number. Collection—Cambridge. Wing 98, tail 112, exp. culmen 16, depth at base 11.2, tarsus 32.5, middle toe minus claw 22.8, hind toe with claw 23.3, Bullock. Locality—see notes below. Not sexed—probably an adult male. The old tag reads "*Pipilo macronyx* | Male? Mexico" | Attached is a folded sheet of paper presumably in Bullock's writing which says [follows quote as given by Salvin and Godman, see p. 121]. July 2, 1938.

Here, for the first time, are some measurements which may be considered accurate. The wing measured by van Rossem as 98 mm. is that of a very large *Pipilo*. The tail, measured as 112 mm., is also extreme. The mean and standard error of the mean for the wing of near topotypical *P. e. maculatus* males is 87.83 ± 0.28 and the standard deviation is 0.94. Three times the standard deviation will contain 99.75 per cent of all specimens in this population. Hence the largest wing measurement theoretically possible is $87.83 + 0.28 + 2.82 = 90.93$ mm. Likewise, the longest tail theoretically possible for this popula-

tion = 107.92. The largest bird I have actually examined from the range of *P. e. maculatus* is a male from Honey, Puebla, with a wing of 89.6 mm. and a tail of 105.0 mm. Using the same method of analysis, it is found that the birds inhabiting the western side of the Valley of Mexico have a theoretical extreme wing length of 97.14 mm. and a tail length of 114.91 mm. The largest bird examined from this population has a wing of 94.9 and a tail of 110.0 mm. The type of *Pipilo macronyx* is thus seen to be of a size commensurate with the population of the western side, but significantly larger than typical *P. e. maculatus*.

Bullock is known to have received specimens from Real del Monte, supposedly from a Mr. Morgan (1827:366). This was probably the source of the type of *P. maculata*. Bullock himself never visited Real del Monte. Because Swainson listed Real del Monte as a locality for *P. macronyx* it has since been assumed that both "*P. maculata*" and "*P. macronyx*" occurred there side by side; hence they were regarded as "good" sympatric species. This, however, is not true. In July, 1946, when I collected in this vicinity in the Sierra de Pachuca, I found one freely interbreeding population, all individuals of which are referable to Swainson's *P. maculata*. Similarly, specimens taken by Nelson and Goldman in 1893, and Helmuth O. Wagner in February, 1946, in the same general area, show no indication of two sympatric species existing there. I therefore regard as untenable the allocation of the large, yellow-spotted *P. macronyx* to Real del Monte. This must simply be regarded as an error and further significance should not be attached to it.

The possibility that the type of *P. macronyx* came from the range of the population inhabiting the southwestern side of the Valley of Mexico (Mount Popocatepetl) must be considered. Bullock passed through the range of that race both en route to Mexico City and on his return trip to England. He collected at Rio Frio, Mexico, on July 21, 1823, on the return trip, when his carriage broke down and he was forced to await repairs. He comments as follows on the birds collected (1827:444-445): "We were detained till the following day, which afforded me an opportunity of procuring several good birds, among them the crimson-throated humming bird, which I never met with but in high cold situations. . . . We shot here also a curious variety of the golden-winged woodpecker, a fine blue species of motacilla, and two kinds of blue jays, all undescribed." Nothing is mentioned of the towhee. Furthermore, if we are to believe Bullock's note on the type, he never saw it east of Mexico City but only "between Mexico (City) and St. Miguel." It is therefore reasonably certain that the type of *macronyx* did not come from the southeastern side of the Valley of Mexico. This area is therefore eliminated from further consideration.

By combining the information given by several authors we arrive at the following description of the type of *macronyx*: upper plumage olive green; wing coverts tipped with yellow or yellowish white; three outer rectrices with terminal spots of greenish or yellowish white, this spot an inch long on the

outermost rectrix; interscapular region streaked with blackish and feathers of scapular region spotted with greenish white or yellowish white; head and throat black; abdomen white; flanks rufous; bend of the wing yellow. Wing 98 mm.; tail 112 mm.

There remains the question of clearly identifying this bird with a known population. The size argues in favor of the population of the western side of the Valley of Mexico. All the color characters are found in this population, but not all are found in the birds of the Pachuca region to the east in Hidalgo. In 54 adult specimens from southern Hidalgo and adjacent localities in Puebla, none can be described as olive green or as having yellowish spots. In 2 of them I can see traces of greenish edges on wing and tail feathers and a faint cloudiness of the white spots caused by the greenish tinge to the plumage, but this is not sufficient to account for the description of the type of *macronyx*. The interscapular region of Hidalgo birds could be described as brown streaked with black, but never as green streaked with black. The latter is an exact description of many individuals from the western side of the Valley of Mexico, however. Many specimens of that population (16 out of 26) have spots on the rectrices an inch or more long. The bend of the wing in all birds from the western side is bright yellow. In 2 out of 54 from Hidalgo I can see a faint yellowish wash. The other 52 are pure white. In other characters (flanks, head, and throat) the difference between the two populations is not sufficient to be significant in making comparisons from a written description (see fig. 18).

The critical characters of the type of *macronyx* do not, then, occur in the Hidalgo population. This fact, together with the discrepancy in size and Bullock's notation that he saw the bird named as the type of *macronyx* only on the western side of the Valley of Mexico, makes certain the identification of *Pipilo macronyx* Swainson with the population of the latter area. It is proper, therefore, to designate *Pipilo virescens* Hartlaub a synonym of *Pipilo macronyx* Swainson. The type locality of *Pipilo macronyx* Swainson may be restricted to the western slope of the Volcán de Toluca—this because Bullock saw it only between Mexico City and San Miguel (*not* Temascaltepec) and because the bird occurs there today and is the most likely source of the two individuals described as types by Swainson.

Nothing heretofore has been said about the second specimen which Swainson thought might be the female. Because of its color characters alone, regardless of its size or Bullock's travels, it could only have come from the population of the western side. If Swainson had described the second specimen, instead of the more spotted bird, as the type, many of the present nomenclatural complexities would never have arisen.

The results of the reallocation of names are as follows:

1. *Pipilo maculata* Swainson becomes *Pipilo erythrophthalmus maculatus* Swainson with type locality at Real del Monte, Hidalgo.

2. *Pipilo macronyx* Swainson becomes *Pipilo erythrophthalmus macronyx* Swainson with restricted type locality the western slope of the Volcán de Toluca, state of México.

3. *Pipilo virescens* Hartlaub becomes a synonym of *Pipilo macronyx* Swainson.

4. The population inhabiting the southeastern side of the Valley of Mexico (Mount Popocatepetl), which has long been erroneously called *Pipilo macronyx macronyx*, is actually nameless.

ACCOUNTS OF SUBSPECIES

Diagnoses for the recognizable geographic races of *Pipilo erythrophthalmus* and *Pipilo ocai* south of the United States are here included. Ten races of *erythrophthalmus* and five of *ocai* are recognized. Three new races are described. Two type localities are restricted: that of *P. o. ocai* to Las Vigas, Veracruz; and that of *P. e. macronyx* to the western slope of the Volcán de Toluca, México.

Abbreviations used in designating the source of specimens examined are as follows:

USBS	United States Bureau of Biological Survey (now the Fish and Wildlife Service)
USNM	United States National Museum
MCZ	Museum of Comparative Zoölogy, Harvard University
AMNH	American Museum of Natural History, New York
MZUM	Museum of Zoölogy, University of Michigan
CNHM	Chicago Natural History Museum
LSU	Louisiana State University
CU	Cornell University
KU	Museum of Natural History, University of Kansas
GMS	George M. Sutton Collection
MVZ	Museum of Vertebrate Zoölogy, University of California

Pipilo erythrophthalmus *gaigei* Van Tyne and Sutton

Pipilo maculatus megalonyx, Ridgway (1901:416), part.

Pipilo maculatus arcticus, Montgomery (1905:15), part.

Pipilo maculatus montanus, Smith (1919:164), part.

Pipilo maculatus gaigei Van Tyne and Sutton (1937:102).

Type.—Adult male, no. 86309, Museum of Zoölogy, University of Michigan; southeast of Boot Spring, 6,800 feet, Chisos Mountains, Brewster County, Texas, May 22, 1932; collected by Josselyn Van Tyne.

Diagnosis.—Male similar to *P. e. montanus* but rump less black, more grayish; dorsal white reduced. Similar to *P. e. arcticus* but dorsal white reduced and flanks paler. Similar to *P. e. griseipygus* but upper tail coverts darker and rump more evenly dark gray, not as admixed with black. Similar to *P. e. orientalis* but rump grayer and flanks paler. For comparisons of size see figures 3 and 4 and table 2.

Distribution.—The Chisos Mountains of Texas northwest to southwestern New Mexico. Specific localities mentioned by Van Tyne and Sutton (1937:103) are as follows:

TEXAS: *Brewster County*: Marathon; Chisos Mts.; Mount Ord; 5 mi. S Alpine [this specimen seems to me to be a wintering *P. e. montanus*]; 15 mi. NE Marathon; Glass Mts.; Peña Blanca Mts. (no specimens listed). *Jeff Davis County*: Davis Mts.

NEW MEXICO: *San Miguel County*: Cabra Spring. *Lincoln County*: Capitan. *Guadalupe County*: Santa Rosa.

Specimens examined.—Total, 10 breeding specimens (♂♂, 6; ♀♀, 4), all from Chisos Mountains (MZUM): Boot Spring, 6,400 ft., 1 im. ♂; Boot Spring, 6,500 ft., 1 ad. ♂, 1 im. ♂; Boot Spring, 6,600 ft., 1 ♀; Blue Creek Canyon, 6,900 ft., 1 ad. ♂; Head of Blue Creek Canyon, 1 ♀; Laguna, 1 ad. ♂, 1 ♀; S Emory Peak, 6,700 ft., 1 im. ♂; Basin, N Emory Peak, 1 ♀.

Habitat.—Van Tyne and Sutton (1937:103) found this race "common" in the Chisos Mountains, where they observed it throughout the forested areas. "It is much more abundant above 6,000 feet than at lower altitudes. . . In winter there were a few in the live-oak groves of the region immediately south and west of Alpine."

TABLE 2
MEASUREMENTS OF *Pipilo erythrophthalmus gaigei*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing...	♂	3	86.53±0.99	1.72	1.98
	♀	4	83.75±1.83	3.66	4.37
Tail.....	♂	3	99.33±2.58	4.48	4.51
	♀	4	96.00±2.87	5.77	6.01
Bill from nostril.. . . .	♂	3	10.10
	♀	4	9.70±0.23	0.45	4.69
Bill depth.....	♂	6	8.20±0.07	0.17	2.04
Tarsus	♂	3	26.86
	♀	4	25.40±0.15	0.29	1.16
Hind toe with claw....	♂	3	21.06±0.17	0.31	1.46
	♀	4	20.40±0.41	0.82	4.00

Discussion.—The clear, dark-gray rump, and pale flanks of *gaigei* separate it from *orientalis* of the Sierra Madre Oriental. It is possible that *gaigei* may be the race inhabiting the Del Carmen Mountains across the Rio Grande from the Chisos. Marsh (MS) recorded a specimen from Vivoras Canyon in the Del Carmens taken on August 25, 1936, under *P. m. montanus*. I have not seen this specimen. The uninhabitable desert areas between the northern end of the Sierra Madre Oriental near Monterrey and the Del Carmens provide an ample barrier between *gaigei* and *orientalis*. It is possible that the Rio Grande itself is the southern barrier for *gaigei* and that *orientalis* may extend north into the Del Carmens.

The solidly black rump of *P. e. montanus* separates it from *gaigei*. Since the present paper is restricted to the area south of the Mexican border, a detailed study of *montanus* in the United States has not been made.

P. e. gaigei does not come into contact with *P. e. griseipygus* of the southern Sierra Madre Occidental. The two races are separated by a large area of unfavorable country in southeastern Chihuahua and eastern Durango.

Pipilo erythrophthalmus orientalis*, new subspecies?Pipilo oregonus*, (not of Bell) Duges (1868:140), part.*Pipilo maculatus maculatus*, Ridgway (1901:410), part.*Pipilo maculatus megalonyx*, Ridgway (1901:415), part.*Pipilo maculatus montanus*, Phillips (1911:89), part.*Pipilo maculatus gaigei*, Sutton and Burleigh (1939:45), part.

Type.—Adult male, no. 115044, Museum of Vertebrate Zoölogy; 8 miles southeast of Galeana, 6,000 feet, Nuevo León, Mexico, April 23, 1948; collected by Charles G. Sibley, orig. no. 3242.

TABLE 3
MEASUREMENTS OF *Pipilo erythrophthalmus orientalis*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	21	86.33±0.30	1.39	1.60
	♀	24	79.01±0.54	2.64	3.34
Tail.....	♂	20	99.61±0.67	3.00	3.00
	♀	23	91.32±0.91	4.38	4.80
Bill from nostril.....	♂	21	9.99±0.08	0.36	3.65
	♀	24	9.89±0.09	0.33	3.31
Bill depth.....	♂	21	8.36±0.05	0.25	3.04
Tarsus.....	♂	21	27.74±0.19	0.87	3.13
	♀	23	26.77±0.16	0.78	2.93
Hind toe with claw....	♂	20	21.30±0.80	1.13	5.32
	♀	24	20.43±0.19	0.93	4.55

Diagnosis.—Similar to *P. e. gaigei* but rump heavily admixed with black; back clearer black, less grayish; flanks darker. Differs from *P. e. maculatus* in having clear black dorsum, lacking olivaceous color of *maculatus*. Distinguished from *P. e. montanus* by reduction of white dorsally, by darker flanks, and by mottled rump, rather than solidly black rump. Similar to *P. e. griseipygus* but upper tail coverts darker, flanks darker, and general tone of dorsum blacker. For comparisons of size see figures 3 and 4 and table 3.

Distribution.—The Sierra Madre Oriental from the Mesa de Chipinque and Diamante Pass, south to about 22° N. Lat. Specimens of typical *P. e. orientalis* have been examined from 5 miles northeast of Ciudad del Maíz, San Luis Potosí; but specimens from Jacala, Hidalgo, show the effect of the olive dorsal coloration of *P. e. maculatus* and are considered to be intergrades between *orientalis* and *maculatus*. The westerly extent of the range of *orientalis* and its relationship to *griseipygus* are not known.

Specimens examined.—Total, 70 (breeding ♂♂, 28; breeding ♀♀, 13; winter ♂♂, 14; winter ♀♀, 12; juv., 1; unsexed, 2). Localities from which breeding birds have been examined are marked with an asterisk.

NUEVO LEÓN: *Mesa de Chipinque, 5,000 ft., 3 ♂ (OU), 1 ♂ (GMS); Mesa de Chipinque, 7,500 ft., 1 ♂, 1 ♀ (OU); Mesa de Chipinque, 4,000 ft., 10 mi. SW Monterrey, 1 ♂ (MVZ); Mesa de Chipinque, near Monterrey, 5,000 ft., 2 ♂ (OU and USBS); *Cerro de Potosí, 7,000 ft., near Galeana, 4 ♂, 1 ♂ juv., 1 ♀ (MVZ); *Galeana, 6,500 ft., 1 ♀ (CNHM); *8 mi. SE Galeana, 6,000 ft., 16 ♂, 8 ♀ (MVZ).

COAHUILA: *Diamante Pass, 7,500–8,000 ft., near Saltillo, 1 ♂, 1 ♀ (LSU); Saltillo, 6,000 ft., 1 ♀ (LSU); *Sierra de Guadalupe, 3 ♂, 1 ♀ (USBS).

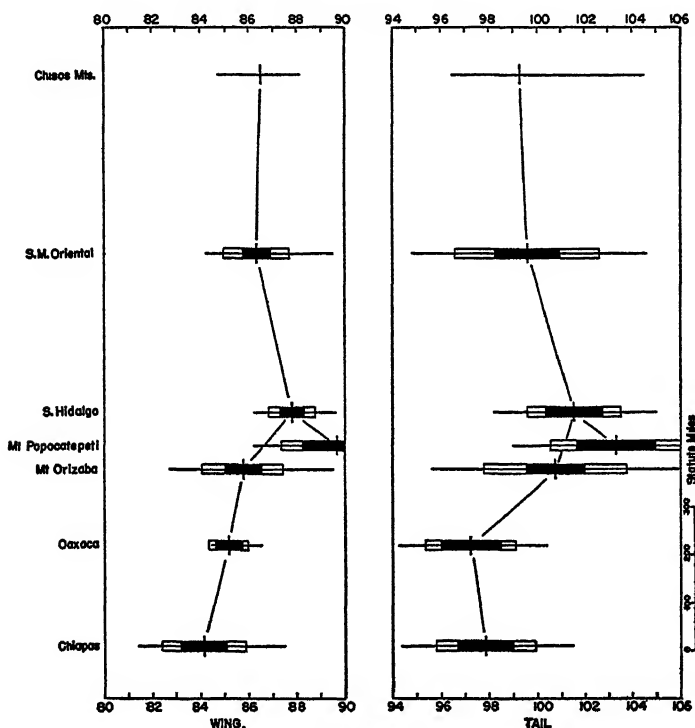


Fig. 3. Statistical analysis of wing and tail lengths (mm.) in some populations of *Pipilo erythrophthalmus*. Horizontal lines represent range; rectangles mark standard deviation with solid black showing twice the standard error of the mean. Note marked influence of *P. e. vulcanorum* (Mount Popocatepetl) on population of *P. e. maculatus* from southern Hidalgo.

TAMAULIPAS: *Miquihuana, 2 ♂ (USBS); *Rancho del Cielo, 3,300 ft., 5 mi. NW Gómez Farías, 1 ♀ (GMS).

SAN LUIS POTOSÍ: 5 mi. NE Ciudad del Maíz, 7 ♂, 11 ♀ (MVZ); 4 mi. W Naranjos, 1,200 ft., 1 ♂ (LSU); *Rancho Miramar Grande, near Xilitla, 5,100 ft., 1 ♂, 1 ♀ (LSU).

The following specimens are not typical. They may be intergrades between *P. e. griseipygius* and *P. e. orientalis* or between *orientalis* and *maculatus*. For the present they are referred to *orientalis*.

SAN LUIS POTOSÍ: *R. R. tracks between Alvarez and San Isidro, 8,000 ft., 1 ♂ (LSU); *San Isidro region, 1 ♀ (LSU); *Cerro Campanario, 8,000 ft., 45 mi. SE San Luis Potosí, 1 ♂, 1 ♀ (LSU); mts. near Jesús María, 2 ♂ (USBS).

GUANAJUATO: Santa Rosa, 1 ♀ (USNM).

Habitat.—This race breeds from 3,300 feet to at least 7,000 feet, and probably higher, in the Sierra Madre Oriental. The optimum altitude range seems to be between 5,000 and 7,000 feet in the breeding season. At the type locality, at an altitude of 6,000 feet, the birds were abundant and breeding in late April. At that level the vegetation (pl. 13, fig. 1) is a dense scrub composed of mesquite, yucca, scrub oak, and other semixerophytes. A few small pines occur, but they are sparse. The race inhabits a similar vegetative association 5 miles northeast of Ciudad del Maíz, San Luis Potosí. On the Mesa de Chipinque, Nuevo León, *orientalis* lives in shrubby undergrowth beneath large oaks and pines. All these situations contrast markedly with the habitat of *P. e. maculatus* in the Sierra de Pachuca described on page 132.

Discussion.—It is not surprising that the population of towhees inhabiting the Sierra Madre Oriental should prove racially separable from the birds of the Chisos Mountains of Texas. A stretch of uninhabitable desert provides a barrier to intermixture of the two populations. The range of *orientalis* is a relatively narrow strip along the eastern edge of the plateau where moisture-laden winds from the Gulf of Mexico deposit enough water to maintain the necessary dense cover. At the same time the altitude is sufficient to meet other ecological requirements of the species. The narrow belt of suitable habitat is bounded on the west by the desert of the interior plateau and on the east by the deciduous subtropical forest of lower elevations.

Pipilo erythrophthalmus maculatus Swainson

Pipilo maculata Swainson (1827:434).

Pipilo maculata Swainson (1838:374).

Pipilo maculatus, Selater (1856:304), part.

[*Pipilo maculatus*] var. *maculatus*, Baird, Brewer, and Ridgway (1874:108), part.

Pipilo arcticus, (not of Swainson) Selater (1862:119), part.

?*Pipilo oregonus*, (not of Bell) Duges (1868:140), part.

Pipilo submaculatus Ridgway (1886:332) (=hybrid *P. o. ocai* × *P. e. maculatus*).

Pipilo complexus Ridgway (1886:332) (=hybrid *P. o. ocai* × *P. e. maculatus*).

Pipilo orisabae Cox (1894:161) (=hybrid *P. o. ocai* × *P. e. maculatus*).

Pipilo maculatus maculatus, Ridgway (1901:410), part.

Type.—Present location unknown. Obtained by Bullock during his residence in Mexico, supposedly from Real del Monte, Hidalgo. Probably collected in the spring of 1823.

Diagnosis.—Distinguished from *P. e. orientalis* by olivaceous tone of dorsum and lack of black in rump. Flanks and upper tail coverts lighter in tone or coloration. From *P. e. oaxacae*, *maculatus* is separated by its blackish-olive dorsum contrasted with browner dorsal tone of *oaxacae*. Edgings of tertials white and narrow in *maculatus*, buffy and broad in *oaxacae*. General size larger, wing longer. From *P. e. vulcanorum*, *maculatus* is separated by reduction of dorsal green, whiter dorsal spots, and smaller size. For comparisons of size see figures 3 and 4 and table 4.

Distribution.—The central eastern highlands in the states of Hidalgo and Puebla. Intergrades in the region of Jacala, Hidalgo, with *P. e. orientalis* and probably about at the Rio Santo Domingo, in northeastern Oaxaca, with *P. e. oaxacae*. The extent of the range of this form to the northwest is in doubt. This may be the race in Guanajuato, but fresh material is needed to determine the status of Guanajuato birds.

TABLE 4
MEASUREMENTS OF *Pipilo erythrophthalmus maculatus*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
HIDALGO					
Wing.....	♂	11	87.83±0.28	0.94	1.07
	♀	23	81.67±0.47	2.27	2.78
Tail.....	♂	11	101.55±0.58	1.93	1.90
	♀	23	94.03±0.79	3.79	4.03
Bill from nostril.....	♂	11	10.41±0.13	0.42	4.06
	♀	24	9.98±0.10	0.51	5.11
Bill depth.....	♂	11	8.73±0.08	0.26	2.94
Tarsus.....	♂	11	29.02±0.32	1.06	3.65
	♀	24	28.39±0.10	1.00	3.51
Hind toe with claw....	♂	11	21.74±0.39	1.30	5.91
	♀	24	20.82±0.19	0.95	4.55
MOUNT ORIZABA					
Wing.....	♂	22	85.79±0.37	1.65	1.92
	♀	19	80.16±0.55	2.42	3.02
Tail.....	♂	23	100.79±0.62	2.93	2.91
	♀	19	93.33±1.03	4.50	4.81
Bill from nostril.....	♂	23	10.28±0.10	0.50	4.87
	♀	19	9.94±0.13	0.57	5.75
Bill depth.....	♂	21	8.39±0.06	0.26	3.12
Tarsus.....	♂	23	28.80±0.19	0.90	3.14
	♀	16	27.99±0.02	1.00	3.56
Hind toe with claw....	♂	23	21.13±0.17	0.80	3.78
	♀	19	20.79±0.24	1.06	5.10

Specimens examined.—Total, 119 (♂♂, 68; ♀♀, 42; juv., 7; unsexed, 2; hybrids, not included in total, 6).

HIDALGO: El Chico, 4 ♂ (USBS); 6 mi. N Pachuca, 9,600 ft., 5 ♂, 7 ♀, 4 juv. (MVZ); Real del Monte, 1 ♂ (MCZ), 1 ♀ (USBS); San Agustín, 2 ♂ (USBS); Irolo, 1 ♂, 1 ♀ (USBS); Tulancingo, 1 ♀ (USBS); Apulco, 2 ♂, 6 ♀, 1 ♀ (MVZ).

PUEBLA: Honey, 2,300 m., 8 ♂, 5 ♀ (MVZ); Beristain, 2,185 m., 2 ♂, 3 ♀ (MVZ); Chalchicomula, 7 ♂, 3 ♀ (USBS); 8 mi. NE Chalchicomula, 10,350 ft., 29 ♂, 14 ♀, 3 juv. (MVZ); Mount Orizaba, 4 ♂, 2 ♀ (USBS).

TLAXCALA: Mount Malinche, 2 ♂ (USBS).

Habitat.—This subspecies inhabits the high-altitude mixed forest in the mountainous portions of its range. In the vicinity of the type locality at Real del Monte, Hidalgo, it is found in the pine-oak-fir woodland. Thickets of juniper and *Baccharis* are used as cover; the higher trees afford song perches (pl. 13, fig. 2). *P. e. maculatus* is absent from the brushy areas at lower elevations where taller trees are lacking. This habitat preference is similar to that

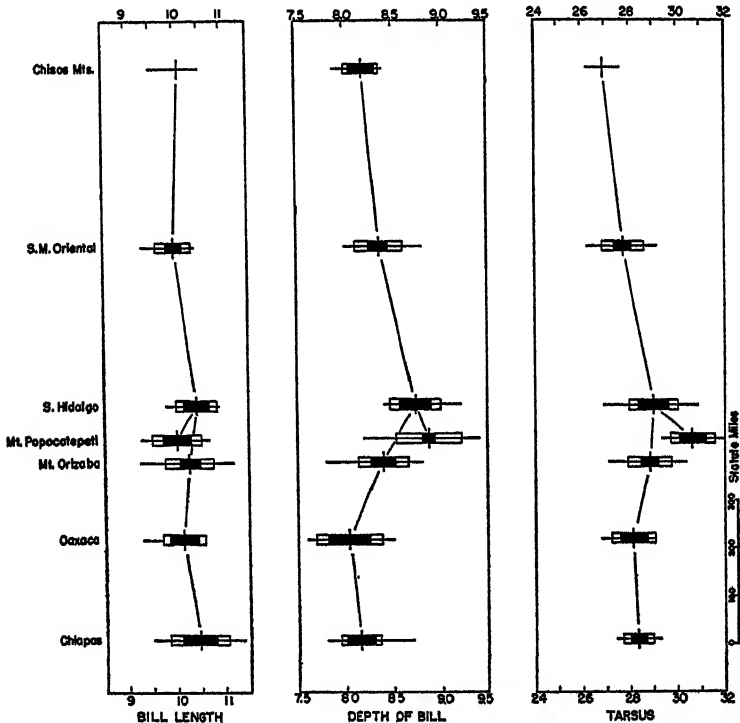


Fig. 4. Statistical analysis of bill and tarsal measurements in some populations of *Pipilo erythrophthalmus*. Different proportions of bill length to depth between pure races and mixed groups of transplateau gradient indicated by relationships of populations of Mount Popocatepetl to those of southern Hidalgo.

of the greenest races of *P. erythrophthalmus* (*vulcanorum* and *macronyx*) in the states of México and Michoacán and also similar to that of the races of *P. ocai*. It is in contrast to the habitat preferences of more northerly races of *P. erythrophthalmus*.

In Puebla, on the western slope of Mount Orizaba, this race occupies the lower elevations below the coniferous forest. It is most abundant in brushy gullies and in dense, low cover. It enters the margin of the coniferous forest where that forest has been thinned by man and dense ground cover is available. At 10,300 feet, above Chalchicomula, for example, this race enters the coniferous forest for about half a mile, which is the average distance that

thinning, but not complete removal of the forest, has progressed. In this narrow belt the birds occupy thickets of *Baccharis conferta*, *Salix otylepis*, *Eupatorium glabratum*, *Lupinus montanus*, *Senecio cinerarioides*, *Senecio salignus*, and small oaks and conifers. In this border habitat (pl. 14, fig. 1) they are in contact with *P. o. ocai*, which occupies the same thickets and utilizes the same plants as cover, nest sites, and song posts.

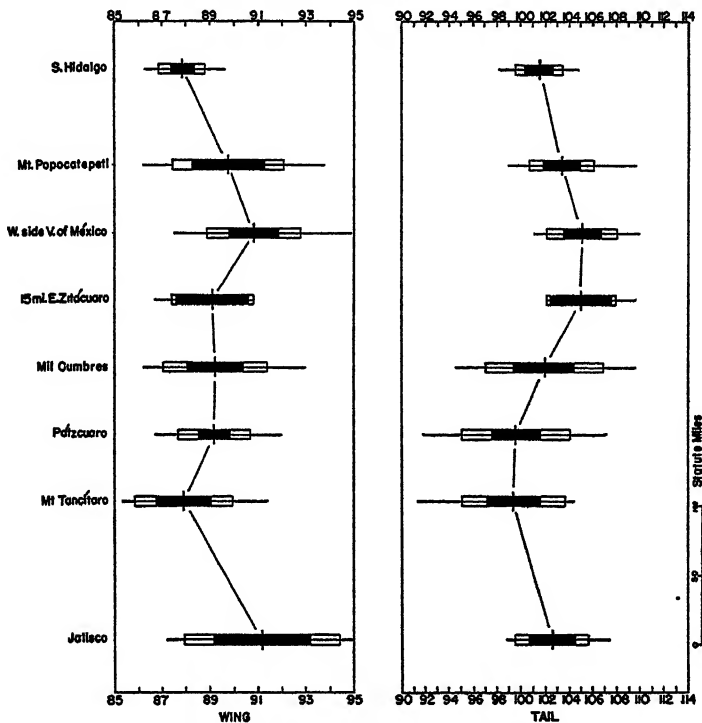


Fig. 5. Statistical analysis of wing and tail lengths in transplateau series of populations. There is not a striking size gradient comparable to color gradient shown by figs. 17 and 18. See map, fig. 16, for geographical relationships of populations.

Discussion.—The occupancy by this race of the high-altitude coniferous forest at Real del Monte, Hidalgo, and other localities in that vicinity is seemingly correlated with the effect of contact with *P. e. vulcanorum* from the south. The color and size of *P. e. maculatus* in the Real del Monte area are obviously affected by *P. e. vulcanorum* (see figs. 3, 4, and 17), and the evidence is strong that the more intangible factor of habitat preference is also influenced. *P. e. orientalis* is, like most other races of *P. erythrophthalmus*, a bird of the scrub thickets. Similarly, *P. e. oaxacae* inhabits brushy cover at middle altitudes, and the population of *P. e. maculatus* on the western slope of Mount Orizaba does likewise. Only in the Real del Monte area, where the maximum influence of *vulcanorum* would be expected, does *P. e. maculatus*

inhabit an alpine forest association. This population is actually an intergrading one between *P. e. vulcanorum* and the more stable populations to the north and southeast. For this reason I consider it unwise to name the Mount Orizaba birds, although in some measurements (figs. 3 and 4) and in color tones they are significantly different from topotypical *P. e. maculatus*.

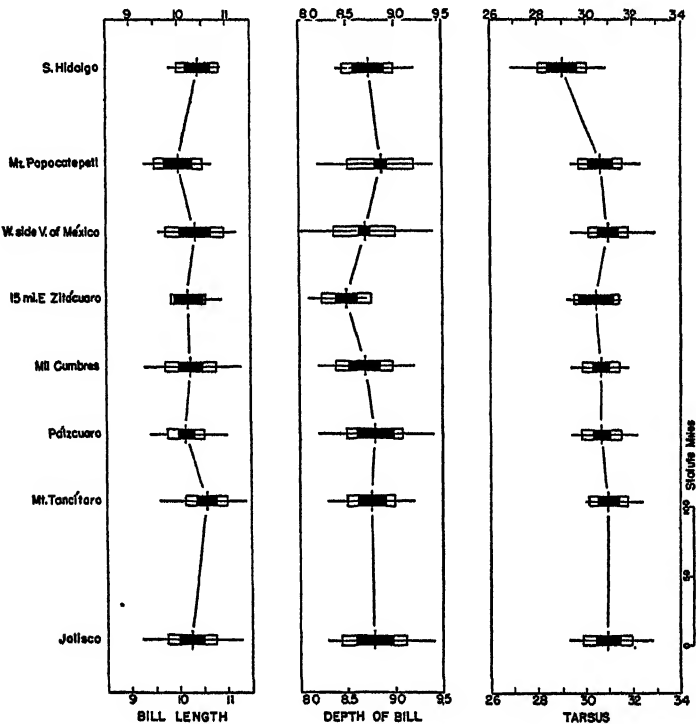


Fig. 6. Statistical analysis of bill and tarsal measurements in trans-plateau series of populations. See map, fig. 16, for geographical relationships of populations.

Pipilo erythrophthalmus *oaxacae*, new subspecies

Pipilo maculatus, Sclater (1858:304), part.

Pipilo maculatus maculatus, Ridgway (1901:410), part.

Type.—Adult male, no. 115141, Museum of Vertebrate Zoölogy; La Cumbre, 9,000 feet, 5 miles northeast of Cerro San Felipe, Oaxaca, Mexico, April 4, 1948; collected by Charles G. Sibley, orig. no. 3173.

Diagnosis.—Similar to *P. e. maculatus* but dorsal coloration lighter and browner, that is, dorsal black reduced; rump more brownish; dorsal white more extensive, especially noticeable on edges of tertials; general size smaller; wing shorter. Similar to *P. e. orientalis* but dorsal tones brown and buffy rather than jet black; rump clear brownish olive, not suffused with black as in *orientalis*. For comparisons of size see figures 3 and 4 and table 5.

Distribution.—The highland areas of Oaxaca, probably from the vicinity of Tamazulapan, southeast to Mount Zempoaltepec. Probably intergrades with *P. e. maculatus* in the northeastern part of Oaxaca about at the Rio Santo Domingo.

Specimens examined.—Total, 30 (♂♂, 18; ♀♀, 9; juv., 3).

OAXACA: 10 mi. NE Cerro San Felipe, 7,400 ft., 2 ♂, 1 juv. (MVZ); La Cumbre, 9,000 ft., 5 mi. NE Cerro San Felipe, 11 ♂, 7 ♀ (MVZ); Cerro San Felipe, 2 ♂, 1 ♀ juv. (USBS); Cerro San Felipe, 2,100 m., 1 ♀ (MVZ); Mount Zempoaltepec, 1 ♂, 1 ♂ juv. (USBS); Reyes, 1 ♀ (USBS); Cieneguilla, 1 ♂ (USNM); La Parada, 1 ♂ (USNM).

TABLE 5
MEASUREMENTS OF *Pipilo erythrophthalmus oaxacae*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	9	85.19±0.27	0.82	0.96
	♀	11	80.47±0.68	2.24	2.79
Tail.....	♂	9	97.22±0.62	1.86	1.91
	♀	11	91.12±1.02	3.40	3.73
Bill from nostril.....	♂	9	10.14±0.15	0.45	4.46
	♀	11	9.87±0.12	0.41	4.15
Bill depth.....	♂	9	8.04±0.11	0.33	4.08
Tarsus.....	♂	9	28.16±0.30	0.92	3.25
	♀	11	28.07±0.23	0.76	2.73
Hind toe with claw....	♂	9	20.67±0.23	0.70	3.40
	♀	11	19.59±0.26	0.85	4.35

Habitat.—The ecological requirements of *P. e. oaxacae* are discussed on pages 152–154.

Discussion.—*P. e. oaxacae* is a surprisingly well-marked race considering the relatively short distance between Mount Orizaba and Cerro San Felipe. There is probably a significant geographical barrier at the valley of the Rio Santo Domingo which has permitted *oaxacae* to differentiate. I am not personally familiar with the detailed topography of that region, but maps of the area indicate the presence of a rather large area of low elevation. This would presumably be a barrier to *P. erythrophthalmus*.

The population of *P. e. maculatus* of Mount Orizaba is roughly intermediate between *oaxacae* and topotypical *maculatus*. This is apparently due to the influence of *vulcanorum* on the Real del Monte population, causing it to differ from the Mount Orizaba birds. I have referred the Mount Orizaba birds to *maculatus* because they seem to fall closer to that population, and the wisdom of naming them is doubtful under the circumstances.

To the south and east, the Isthmus of Tehuántepec is at present a total barrier to the species, which has permitted the differentiation of *P. e. chiapensis* from *P. e. oaxacae*. *P. e. oaxacae* shows characters in common with *P. e. chiapensis*, principally in the large amounts of brown and buff dorsally.

The westward extent of *P. e. oazacae* is unknown. To the east it is sharply limited by unsuitable conditions as the mountains drop away into the lowlands of Veracruz.

***Pipilo erythrophthalmus chiapensis* van Rossem**

Pipilo maculatus maculatus, Ridgway (1901:410), part.

Pipilo maculatus chiapensis van Rossem (1938:130).

Type.—Adult male, no. 99.2.1.3480, British Museum; San Cristóbal, Chiapas, Mexico, May 14, 1897; collected by W. B. Richardson.

TABLE 6
MEASUREMENTS OF *Pipilo erythrophthalmus chiapensis*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	13	84.06±0.47	1.70	2.02
	♀	7	77.12±0.97	2.56	3.31
Tail.....	♂	13	97.88±0.67	2.04	2.09
	♀	7	88.88±0.90	2.36	2.65
Bill from nostril.....	♂	13	10.46±0.17	0.61	5.80
	♀	7	10.21±0.12	0.33	3.22
Bill depth.....	♂	11	8.15±0.07	0.20	2.52
Tarsus.....	♂	13	28.33±0.17	0.63	2.21
	♀	7	27.35±0.13	0.34	1.25
Hind toe with claw....	♂	12	20.24±0.21	0.73	3.60
	♀	7	19.12±0.23	0.60	3.15

Diagnosis.—Similar to *P. e. oazacae* but all colored areas darker. (See diagnosis of *P. e. oazacae*.) Similar to *P. e. repetens* but flanks darker, back more buffy, and dorsal spotting more heavily clouded with brown. For comparisons of size see figures 3 and 4 and table 6.

Distribution.—The highlands of north-central Chiapas from San Cristóbal to Comitán.

Specimens examined.—Total, 26 (♂♂, 18; ♀♀, 7; unsexed, 1).

CHIAPAS: 4 mi. NW San Cristóbal, 7,700 ft., 9 ♂, 5 ♀ (MVZ); San Cristóbal, 2 ♂, 1 ♀, 11? (USBS); 2 mi. S San Cristóbal, 2,100 m., 1 ♂ (UMMZ); Comitán, 1,700 m., 2 ♂ (UMMZ); near Comitán, 1 ♂ (USBS); 20 mi. SE Teopisca, 1 ♂ (USBS); Canjob, 1 ♀ (USBS); Todos Santos, 1 ♂ (USBS); 2 mi. W Zinacantan, 1 ♂ (UMMZ).

Habitat.—In the highlands of north-central Chiapas, as at the type locality, *P. e. chiapensis* is abundant in dense brushy cover associated with the pine-oak forest. The principal shrub is a *Baccharis* which occurs as an understory plant and forms chaparral areas on open hillsides. A few madrones (*Arbutus*) are scattered through the dominant pines and oaks. Plate 15, figure 2, illustrates the aspect of towhee habitat 4 miles northwest of San Cristóbal las Casas, at 7,700 feet altitude.

Discussion.—*P. e. chiapensis* is a well-differentiated race apparently restricted to the highlands of northern Chiapas. It is limited on the west by the low country of the Isthmus of Tehuán-tepec and on the north by the abrupt drop-off toward the Gulf lowlands. It is apparently separated from *P. e. repetens* of the Pacific cordillera by intervening lowland areas. It is possible that *chiapensis* and *repetens* intergrade near the Chiapas-Guatemala border at about 16° N. Lat.

Pipilo erythrophthalmus repetens Griscom

Pipilo oregonus, (not of Bell) Salvin (1866:193), part.

Pipilo maculatus, (not of Swainson) Salvin and Godman (1886:408), part.

Hortulanus maculatus, Dearborn (1907:117), part.

Pipilo maculatus repetens Griscom (1930:12).

Type.—Adult male, no. 59,025, Dwight Collection; Zanzón, 8,000 feet, western Guatemala, January 8, 1925; collected by A. W. Anthony.

Diagnosis.—Similar to *P. e. chiapensis* but flanks lighter, back more blackish olive (not buffy as in *chiapensis*), white dorsal spots less clouded with brown. Similar to *P. e. oaxacae* but darker dorsally.

Distribution.—The Pacific cordillera of Guatemala, and Volcán Tacaná, Chiapas, Mexico.

Specimens examined.—Total, 9 (♂♂, 6; ♀♀, 3).

GUATEMALA: Tecpam, 8,600 ft., Sierra Santa Elena, 1 ♂ (USNM); Tecpam, 9,000 ft., Sierra Santa Elena, 1 ♀ (USNM); Tecpam, 9,500 ft., Sierra Santa Elena, 1 ♂ (USNM); Chichivac, 8,600 ft., Tecpam, 1 ♀ (USNM); Santa María de Jesús, N face Volcán de Agua, 7,800 ft., 1 ♂ (USNM); Nebaj (?), Quitche, 1 ♀ (USNM); Nspantan (?), Quitche, 1 ♂ (USNM).

CHIAPAS: Chiquihuite, 2,500 m., Volcán Tacaná, 1 ♂ (UMMZ); Volcán Tacaná, 3,950 m., 1 ♂ (UMMZ).

Habitat notes.—Griscom (1932:367) records this race as "A common bird in the highlands from 6,000 to 10,500 feet." Wetmore (1941:580) found them in weed-grown fields at 7,800 feet, and noted them as common from 8,600 feet to 10,000 feet in thickets but not in forests.

Discussion.—This race is included in the present paper to round out the distributional picture south of the United States. Griscom (1932:367) lists a number of additional Guatemalan localities. The relationships of *chiapensis* and *repetens* need further delineation.

Pipilo erythrophthalmus montanus Swarth

Pipilo arctica, Woodhouse (1853:81), part.

Pipilo maculatus megalonyx, Allen (1893:39), part.

Pipilo maculatus montanus Swarth (1905:172), part.

Type.—Adult male, no. 40,625, California Academy of Sciences; Miller Canyon, Huachuca Mountains, Arizona, May 20, 1903; collected by Harry S. Swarth, orig. no. 3972.

Diagnosis.—*P. e. montanus* is separable from *griseipygius* by intense, deep black of dorsum (back, rump, and upper tail coverts) contrasted with grayer and more olivaceous dorsal coloration of *griseipygius*. From *P. e. gaigei*, *montanus* is distinguished by deep black rump, contrasted with clear dark-gray rump of *gaigei*; dorsal white more extensive and flanks darker than in *gaigei*. Similar to *P. e. orientalis* but dorsal white more extensive and rump solidly black rather than only streaked with black as in *orientalis*.

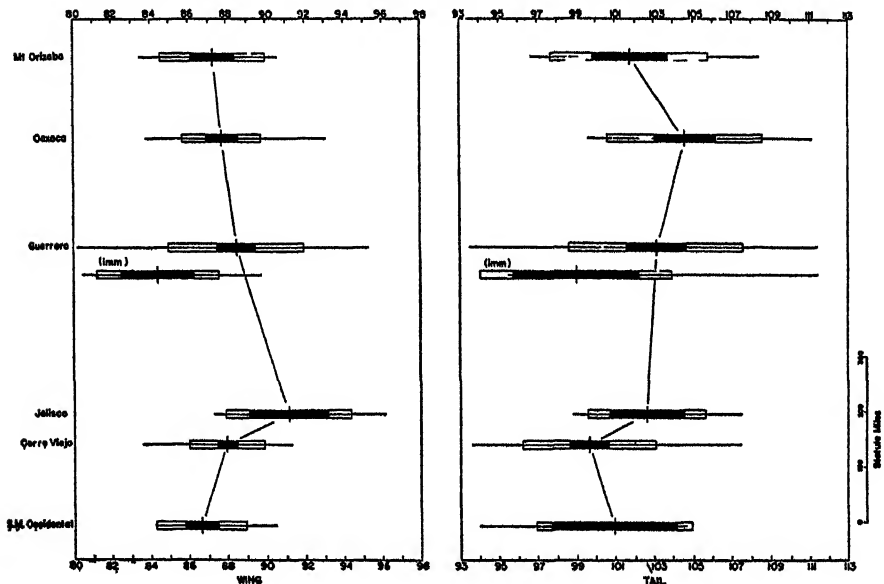


Fig. 7. Statistical analysis of wing and tail lengths for some races of *Pipilo ocai*, Cerro Viejo hybrid population, and *P. e. griseipygius* (Sierra Madre Occidental). Latter is included for comparison with populations of Cerro Viejo and Jalisco. Immature Guerreran specimens are included for comparison with mixed sample of adults and undetectable spring immatures (see p. 147).

Distribution.—In Mexico only in the northern Sierra Madre Occidental, from the border south to about 29° N. Lat., where it intergrades with *P. e. griseipygius*.

Specimens examined.—Total of 159 adults from all parts of the range; 44 adults from Arizona and northern Sonora were used to establish the racial characteristics.

CHIHUAHUA: San Diego, 1 ♀ (AMNH); Colonia García, 3 ♂, 1 ♀ (USBS); San Luis Mts., 1 ♂ (USBS). Specimens from Chihuahua City, 30 mi. W Mifaca, and Rio Chico are intermediate between *montanus* and *griseipygius* but seem closer to *montanus*.

SONORA: Casita, 40 km. S Nogales, 3,300 ft., 14 ♂, 7 ♀ (MVZ).

Pipilo erythrophthalmus griseipygius van Rossem

Pipilo maculatus megalonyx, Miller (1906:172), part.

Pipilo maculatus montanus, Bailey and Conover (1935:423), part.

Pipilo maculatus griseipygius van Rossem (1934:482).

Type.—Adult male, no. 222,899, Museum of Comparative Zoölogy; Jesús María, Chihuahua, undated but probably the fall of 1884; collected by R. R. McLeod.

Diagnosis.—Similar to *P. e. montanus* but upper tail coverts grayer and rump olivaceous black. In *montanus*, back, rump, and upper tail coverts are solid deep black. Similar to *P. e. gaigei* but with more olive, less gray, in rump; flanks of *gaigei* paler and back blacker than in *griseipygius*. Similar to *P. e.*

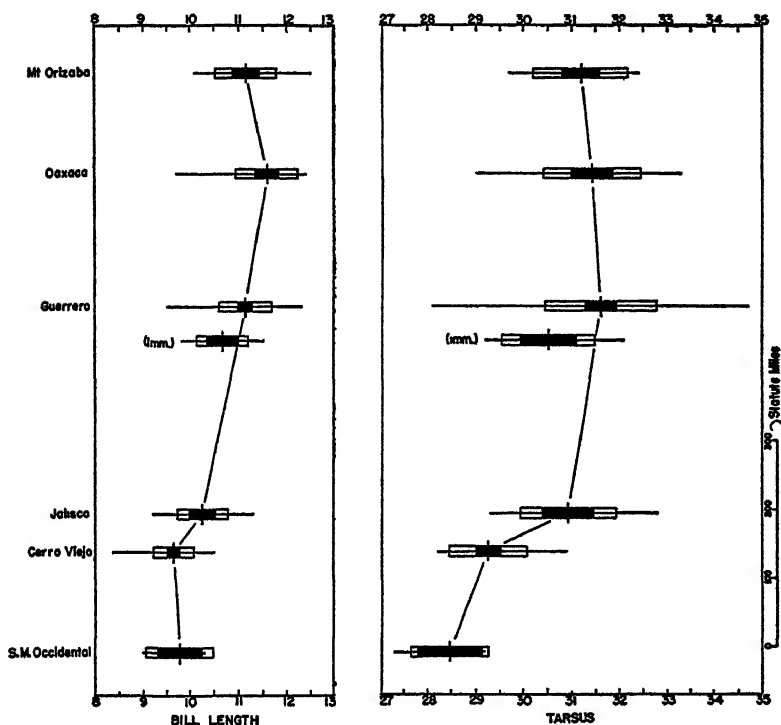


Fig. 8. Statistical analysis of bill and tarsal lengths in some races of *Pipilo ocai*, hybrid population of Cerro Viejo, and *P. e. griseipygius* (Sierra Madre Occidental). See legend, fig. 7.

maculatus but flanks slightly darker and rump and upper tail coverts grayer, less olive. Similar to *P. e. orientalis* but much lighter dorsally. Flank color of *griseipygius* and *orientalis* about the same, both darker than in *gaigei*. For comparisons of size see figures 7 and 8 and table 7.

Distribution.—The Sierra Madre Occidental of western Mexico from about 29° N. Lat., in central Chihuahua, south to southern Durango and northern Nayarit at about 22° N. Lat. Intergrades with *P. e. montanus* in the north. The southern limits of range and relationships with *P. e. maculatus* and *P. e. orientalis* are not known, although in coloration this race is closer to *P. e. maculatus*.

Specimens examined.—Total, 13 (♂♂, 8; ♀♀, 3; juv., 2). Specimens from

Chihuahua City, and 30 miles west of Miñaca, Chihuahua, are intermediate between *griseipygius* and *montanus*.

DURANGO: Ciénega de las Vacas, 8,500 ft., 1 ♂ (AMNIT); Laguna del Progreso, 90 mi. NW Durango, 1 ♂, 1 ♀ (GMS).

SINALOA: El Batel, 5,100 ft., 70 km. NE Mazatlán, 3 ♂, 2 ♀ (MVZ).

ZACATECAS: Plateado, 1 ♂ (USBS).

NAYARIT: Santa Teresa, 2 ♂, 2 ♂ juv. (USBS).

Habitat.—The distribution of *griseipygius* corresponds to the limits of the pine-oak association in the Sierra Madre Occidental south of approximately 29° N. Lat. Pitelka (MS) found this race uncommon at El Batel, 5,100 feet altitude, in Sinaloa. The birds were in undergrowth and thickets where the

TABLE 7
MEASUREMENTS OF *Pipilo erythrophthalmus griseipygius*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	6	86.60±0.94	2.32	2.67
Tail.....	♂	6	100.88±1.61	3.95	3.92
Bill from nostril.....	♂	6	9.78±0.23	0.57	5.87
Tarsus.....	♂	6	28.46±0.29	0.71	2.50

pine-oak woodland was fairly dense. The thickets included *Rubus*, *Rosa*, bushy composites, "pokeberry," and several kinds of ferns.

Discussion.—With so few good specimens available it is difficult to make any but general comments about this race. It is apparently limited on the south by the drop in elevation at the Rio Santiago, on the east by the interior deserts, and on the west by the coastal lowlands.

Although *griseipygius* may have contributed the *erythrophthalmus* component of the Cerro Viejo hybrid population, it is also possible that birds from east of Cerro Viejo did so. The barrier of the low country associated with the Rio Santiago would seem to be more complete than the lowland barrier separating Cerro Viejo from the nearest *P. o. alticola*. Since the Cerro Viejo population is more like *erythrophthalmus* than like *ocai* (see fig. 15), it would seem likely that the source of *erythrophthalmus* influence must be closer to Cerro Viejo than the nearest population of *griseipygius* is known to be.

Pipilo erythrophthalmus vulcanorum, new subspecies

Pipilo macronyx macronyx, Ridgway (1901:409), part.

Type.—Adult male, no. 96755, Museum of Vertebrate Zoölogy; northwestern side of Mount Popocatepetl, 9,700 feet, México, July 19, 1946; collected by Charles G. Sibley, orig. no. 2939.

Diagnosis.—Similar to *P. e. maculatus* but greener dorsally with prominent

black shaft streaks. White spots of wings, back, and tail slightly clouded with yellowish because of increased greenness of general plumage; size and amount of spots only slightly reduced. Size larger. Similar to *P. e. macronyx* but more olivaceous, not so bright green above; spotting of wings, back, and tail more prominent than in *macronyx*; more black in dorsal plumage, causing head to merge gradually with dorsal coloration rather than to be sharply delimited as in *macronyx*. For comparisons of size see figures 5 and 6 and table 8.

Distribution.—The mountains forming the southeastern side of the Valley of Mexico, principally the volcanoes Popocatepetl and Ixtaccihuatl.

TABLE 8
MEASUREMENTS OF *Pipilo erythrophthalmus vulcanorum*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	10	89.74±0.75	2.36	2.63
	♀	5	84.76±1.16	2.61	3.07
Tail.....	♂	11	103.32±0.83	2.77	2.68
	♀	5	96.20±2.12	4.75	4.94
Bill from nostril.....	♂	10	10.01±0.15	0.50	4.90
	♀	4	9.65±0.21	0.42	4.36
Bill depth.....	♂	10	8.86±0.03	0.35	3.99
Tarsus... ..	♂	11	30.65±0.28	0.92	3.00
	♀	5	29.04±0.74	1.65	5.67
Hind toe with claw....	♂	11	22.67±0.25	0.83	3.66
	♀	5	21.22±0.61	1.35	6.40

Specimens examined.—Total, 19 (♂♂, 12; ♀♀, 6; juv., 1).

MÉXICO: 55 km. SE Mexico City, 10,500 ft., 3 ♂, 1 ♀ juv. (MVZ); NW side Mount Popocatepetl, 9,700 ft., 1 ♂, 2 ♀ (MVZ); W slope Mount Popocatepetl, 11,500 ft., 2 ♂ (GMS); Mount Popocatepetl, 1 ♂ (USBS); Amecameca, 1 ♂ (LSU); 12 km. ESE Amecameca, 11,500 ft., 1 ♀ (KU); 1 ♂, 2 ♀ (USBS); Rio Frio, 11,000 ft., 1 ♂ (GMS).

PUEBLA: Tochimilco, 1 ♂ (USBS).

MORELOS: Tetela del Volcán, 1 ♂, 1 ♀ (USBS).

Habitat.—*P. e. vulcanorum* inhabits the alpine coniferous forest above 8,000 feet. Like all races of the species, it lives in dense thickets and tangles of brushy vegetation. Pines and firs, with some oaks, are the principal trees occurring at the altitudes where *P. e. vulcanorum* is most abundant.

Discussion.—Nomenclatural problems affecting this race are discussed on pages 120–125 in the present paper.

P. e. vulcanorum intergrades to the north with *P. e. maculatus*. The result of this contact is evident in both races. *P. e. maculatus* is larger and greener than *P. e. orientalis* to the north, or the population of Mount Orizaba referred to *P. e. maculatus*. *P. e. vulcanorum* has more dorsal spots and larger tail spots than *P. e. macronyx* of the western side of the Valley of Mexico. Intergradation between *vulcanorum* and *macronyx* probably occurs across the southern

end of the Valley of Mexico; the connecting area there is reduced by the low country immediately west of Mount Popocatepetl, which does not provide suitable habitat conditions.

Pipilo erythrophthalmus macronyx Swainson

Pipilo macronyx Swainson (1827:434).

Pipilo macronyx Swainson (1838:347).

Pipilo virescens Hartlaub (1863:228).

Pipilo chlorosoma Baird (1874:105).

Pipilo macronyx virescens, Ridgway (1901:410).

Type.—Not sexed, probably an adult male, no number, Cambridge Collection; collected in 1823 by William Bullock, "between Mexico (City) and San Miguel." Type locality herein restricted to western slope of the Volcán de Toluca, México.

Diagnosis.—Similar to *P. e. vulcanorum* but greener dorsally; spotting of wings, back, and tail reduced; black shaft streaks in dorsum reduced; yellow appearance of spotted areas due to clouding with green of general plumage color. For comparisons of size see figures 5 and 6 and table 9.

Distribution.—From the mountains bordering the southwestern and western side of the Valley of Mexico, west to Michoacán border. Intergrades with *P. o. nigrescens* via the intermediate population of Sierra de Ozumatlán (Mil Cumbres) between Ciudad Hidalgo and the mountains southeast of Morelia, Michoacán.

Specimens examined.—Total, 36 (♂♂, 21; ♀♀, 12; juv., 1; sex ?, 2).

FEDERAL DISTRICT: Santa Rosa, 2,900 ft., 4 ♂♂, 4 ♀♀ (MVZ); La Cima, 3,000 m., 1 ♀ (MVZ); Contreras, 2,000 m., 1 ♂ (MVZ); Canjada de Contreras, 2,500 m., 1 ♂, 1 ♀ (MVZ); Ajusco, 1 ♂ (MCZ); San Bernade, 2,800 m., 1 ♂ (MVZ).

MÉXICO: Las Cruces, 20 mi. W Mexico City, 1 ♂ (OU); Tenango, 1 ♂ (MCZ); Salazar, 1 ♂ juv., 1 ♀ (USBS); 4 mi. W Salazar, 9,500 ft., 1 ♂ (MVZ); N slope Volcán de Toluca, 3 ♂♂ (USBS); 5 mi. E Lerma 1 ♂ (LSU).

MORELOS: Huitzilac, 1 ♂, 2 ♀♀, 1 ♀ (USBS).

MICHOACÁN: 15 mi. E Zitácuaro, 9,500 ft., 6 ♂♂, 4 ♀♀ (MVZ).

Intergrades between *P. e. macronyx* and *P. o. nigrescens* are from the following localities in Michoacán:

MICHOACÁN: 15 mi. ESE Morelia, 7,300 ft., 4 ♂♂, 2 ♀♀ (MVZ); El Temazcal, 7,300 ft., 20 mi. E. Morelia, 2 ♂♂, 1 ♀ (LSU); 30 mi. E. Morelia, 8,500 ft., 7 ♂♂, 8 ♀♀ (MVZ); Puerto Carnica, 9,100 ft., Sierra de Ozumatlán, 1 ♀ (MVZ); Mirador de Los Mil Cumbres, 7,900 ft., Sierra de Ozumatlán, 1 ♂ (MVZ); Sabaneta, 8,000 ft., 6 mi. SSW Ciudad Hidalgo, 2 ♂♂, 1 ♀ (MVZ).

Habitat.—Like *P. e. vulcanorum* and topotypical *P. e. maculatus*, *macronyx* is closely connected with alpine forest association. West of Mexico City it occurs in pine-oak-fir forests from approximately 8,000 to 11,000 feet altitude. The races inhabiting this association are those of the clinal series connecting *P. o. nigrescens* with *P. e. maculatus*.

TABLE 9
MEASUREMENTS OF *Pipilo erythrophthalmus macronyx*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
WESTERN SIDE OF VALLEY OF MEXICO					
Wing.....	♂	14	90.80±0.52	1.94	2.14
	♀	7	86.41±1.31	3.47	4.01
Tail.....	♂	14	105.11±0.80	3.00	2.84
	♀	8	100.07±1.23	3.47	3.46
Bill from nostril.....	♂	15	10.35±0.16	0.61	5.90
	♀	8	10.00±0.14	0.39	3.93
Bill depth.....	♂	14	8.69±0.03	0.32	3.68
	♀	15	30.99±0.22	0.84	2.73
Tarsus.....	♂	15	30.05±0.21	0.61	2.03
	♀	8	22.72±0.30	1.15	5.10
Hind toe with claw....	♂	15	22.33±0.24	0.69	3.10
	♀	8			
15 MILES EAST OF ZITÁCUARO, MICHOACÁN					
Wing.....	♂	5	89.10±0.75	1.70	1.90
	♀	4	83.83±1.36	2.72	3.24
Tail.....	♂	5	105.06±1.25	2.80	2.66
	♀	4	97.13±2.46	4.92	5.07
Bill from nostril.....	♂	6	10.20±0.15	0.37	3.61
	♀	4	10.10±0.24	0.48	4.71
Bill depth.....	♂	5	8.50±0.11	0.25	3.00
	♀	6	30.47±0.37	0.91	3.00
Tarsus.....	♂	6	30.20±0.48	0.95	3.16
	♀	4	22.25±0.41	1.00	4.52
Hind toe with claw....	♂	6	22.25±0.18	0.37	1.66
	♀	4			
MIL CUMBRES					
Wing.....	♂	14	89.20±0.58	2.18	2.45
	♀	13	85.01±0.77	2.79	3.29
Tail.....	♂	14	101.94±1.29	4.81	4.72
	♀	13	97.02±1.04	3.77	3.88
Bill from nostril.....	♂	15	10.25±0.134	0.52	5.10
	♀	13	10.16±0.23	0.82	0.81
Bill depth.....	♂	14	8.68±0.08	0.29	3.36
	♀	16	30.66±0.20	0.80	2.58
Tarsus.....	♂	16	30.36±0.33	1.19	3.93
	♀	13	21.95±0.34	1.37	6.24
Hind toe with claw	♂	16	22.13±0.33	1.18	5.32
	♀	13			

Discussion.—This race has been known under the name *P. macronyx virescens* for many years. The nomenclatural problems affecting it are discussed at length on pages 120–125 in the present paper.

Pipilo ocai ocai (Lawrence)

Pipilo torquata Du Bus (1847:105).

Kieneria torquata, Bonaparte (1855:356).

Chamaospiza torquata, Selater (1858:304), part.

Buarremon ocai Lawrence (1867:126).

Embericoides torquata, Gray (1870:91), part.

Pipilo complexus Ridgway (1886:332) (=hybrid *P. o. ocai* × *P. e. maculatus*).

Pipilo ocai ocai, van Rossem (1940:174).

Type.—Adult male (restricted type), no. 41669, American Museum of Natural History; collected by Rafael Montes de Oca. No type was designated in the original description, but this specimen is the first catalogued of the co-types.

The type locality, according to Montes de Oca's label, should be Jalapa, Veracruz. It has been so restricted by van Rossem (1940:174). Because *P. o. ocai* does not now, and in Montes de Oca's time undoubtedly did not, occur at Jalapa, it is unlikely that the type came from there. Selater (1859:362–369) lists several boreal species as "collected by Señor Raphael Montes de Oca in the vicinity of Jalapa." It is obvious that these boreal forms did not come from Jalapa itself but from the higher country immediately west of the city, probably from the vicinity of Las Vigas at the northern base of the Cofre de Perote, where all the boreal types, including *P. o. ocai*, occur today. Selater (1859:362–369) lists 35 boreal species including *Regulus calendula*, *Sitta pygmaea*, *Setophaga* (= *Myioborus*) *miniata*, *Ptilogonys cinereus*, *Junco cinereus* (= *phaeonotus*), *Cyanocorax coronatus* (= *Cyanocitta stelleri*), *Trogon mexicanus*, and *Columba fasciata*. As further evidence that Montes de Oca collected among the pines, Selater (1859:362–369) wrote as follows in reference to the highland thrush currently known as *Ridgwayia pinicola*: "*Turdus pinicola*...described...from M. de Oca's specimens, which are now in my collection. M. de Oca informed me that he met with but a single pair of this species on the high land among the pines, whence I named it *pinicola*."

Sumichrast (1869:552) records *P. ocai* as occurring exclusively in the pine woods of the alpine region in Veracruz. Chapman (1898:41) collected at Jalapa for three weeks and found no towhees. At Las Vigas he obtained an *ocai*. Sutton and Burleigh (1940:243) and Davis (1945:285) have recently collected *P. o. ocai* at Las Vigas.

In view of this evidence it seems proper to restrict the type locality of *P. o. ocai* to Las Vigas, Veracruz.

Diagnosis.—From *P. o. brunnescens* and *P. o. guerrierensis*, *P. o. ocai* is distinguished by grayer flanks and darker under tail coverts. From *P. o. alticola*, *ocai* is separated by presence of a white median frontal stripe. For comparisons of size see figures 7 and 8 and table 10.

Distribution.—The mountains of eastern Puebla and western Veracruz from the vicinity of Teziutlán south at least to Mount Orizaba and probably to Zoquitlán, Puebla. Zoquitlán is included on the basis of a record by Ferrari-Perez (see Ridgway 1886a:148), and Teziutlán is included because the hybrid *P. complexus* came from there.

Specimens examined.—Total, 50 (♂♂, 25; ♀♀, 16; juv., 3; sex?, 6; 7 hybrids not included in total).

PUEBLA: 8 mi. NE Chalechicomula, 10,350 ft., 19 ♂♂, 13 ♀♀, 1 ♂ juv., 2 sex? (MVZ); Mount Orizaba, 4 ♂♂, 2 ♀♀ (USBS).

VERACRUZ: Near (= 1 mi. S) Las Vigas, 8,500 ft., 1 ♂ (CU); Las Vigas, 8,000 ft., 1 ♂ (AMNH); Cofre de Perote, 1 ♀ (USBS); "Orizaba E. Mexico," 3 unsexed (USNM); "Cerro de Tepoxtlán, Orizaba, Mexico," 1 unsexed (USNM).

TABLE 10
MEASUREMENTS OF *Pipilo ocai ocai*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	23	87.30±0.56	2.70	3.08
	♀	15	81.99±0.72	2.80	3.42
Tail.....	♂	23	101.79±0.95	4.10	4.02
	♀	14	96.36±1.08	4.05	4.20
Bill from nostril.....	♂	22	11.16±0.13	0.62	5.56
	♀	15	10.65±0.09	0.36	3.40
Tarsus.....	♂	23	31.20±0.19	0.89	2.85
	♀	14	30.04±0.22	0.83	2.78
Hind toe with claw....	♂	22	22.89±0.16	0.77	3.38
	♀	15	22.14±0.29	1.13	5.12

Habitat.—The habitat of *P. o. ocai* is the coniferous forest above 8,000 feet, where it occupies brushy thickets and fence rows. For details of habitat relations see pages 152–154, and plate 15, figure 1.

Discussion.—The correct specific name to be applied to this group is in some doubt. The name *torquata* of Du Bus is based on a hybrid and hence has been discarded, but the type is clearly more like Lawrence's *P. ocai* than it is like the other parental source, *P. e. maculatus*. See figure 12 and pages 161–165.

Uncertainty about the generic position of this species is reflected in the list of generic synonyms. This doubt should be allayed by the demonstration in the present paper of its very close affinity to *P. erythrophthalmus*.

Chapman (1923:243–278) expressed the belief that *P. ocai* was merely a "mutant" of *Buarremon* (= *Atlapetes*) *brunneinuchus*. It seems more in keeping with present information to regard the superficial resemblance between *P. ocai* and *Atlapetes brunneinuchus* as owing to parallelism. This opinion has also been expressed by Wetmore (1943:337).

***Pipilo ocai brunnescens* van Rossem**

Pipilo torquatus torquatus, Ridgway (1901:406), part.

Pipilo torquatus brunnescens van Rossem (1938:131).

Pipilo ocai brunnescens, van Rossem (1940:174).

Type.—Adult male, no. 99.2.13845, British Museum; Totontepec, Oaxaca, Mexico, February, 1889; collected by M. Trujillo.

Diagnosis.—Similar to *P. o. ocai* but flanks browner (less gray). Intermediate in this respect between *P. o. ocai* and *P. o. guerrerensis* in which flanks

TABLE 11
MEASUREMENTS OF *Pipilo ocai brunnescens*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	27	87.77±0.40	2.06	2.34
	♀	18	83.98±0.46	1.94	2.31
Tail.....	♂	27	104.61±0.77	3.98	3.80
	♀	18	99.38±0.80	3.38	3.40
Bill from nostril.....	♂	27	11.60±0.12	0.64	5.49
	♀	18	11.13±0.13	0.54	4.85
Tarsus.....	♂	27	31.43±0.21	1.08	3.44
	♀	18	30.08±0.23	0.98	3.27
Hind toe with claw....	♂	27	23.75±0.24	1.26	5.30
	♀	18	23.16±0.25	1.06	4.60

are yet browner. Differs from *P. o. alticola* in well-developed median frontal stripe of white. For comparisons of size see figures 7 and 8 and table 11.

Distribution.—The highlands of Oaxaca; especially well known from the highland area east of the city of Oaxaca, from Cerro San Felipe to Mount Zempoaltepec.

Specimens examined.—Total, 51 (♂♂, 27; ♀♀, 21; sex ?, 1; juv., 2).

OAXACA: La Cumbre, 5 mi. NE Cerro San Felipe, 9,000 ft., 25 ♂♂, 17 ♀♀, 1 ♀ juv. (MVZ); Cerro San Felipe, 2,800 m., 1 ♀ (MVZ); Cerro San Felipe, 1 ♀ juv. (USBS); Oaxaca, 2 ♀♀ (USBS); Mount Zempoaltepec, 1 ♂, 1 ♀, 1 ? (USBS); mts. near Ozolotepec, 1 ♂ (USBS).

Habitat.—See pages 152–154 and plate 15, fig. 1.

Discussion.—This race is confined to the highlands of Oaxaca. Its distribution is insular, in that it is not in contact with other races of the species. On Cerro San Felipe it is sympatric, over a large area, with *P. e. oaxacae*. Because of this situation the two groups are considered to be different species, although hybrids are formed between other pairs of races in other areas in Mexico. These special situations are discussed on pages 152–176 in the present paper.

Pipilo ocai guerrenderensis* van RossemPipilo torquatus torquatus*, Ridgway (1901:406), part.*Pipilo torquatus guerrenderensis* van Rossem (1938:131).*Pipilo ocai guerrenderensis* van Rossem (1940:174).

Type.—Sex not designated, but probably male, no. 99.2.1.3849, British Museum; Omilteme, Guerrero, Mexico, July, 1888; collected by Mrs. H. H. Smith.

TABLE 12
MEASUREMENTS OF *Pipilo ocai guerrenderensis*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
ADULTS					
Wing.....	♂	52	88.45±0.48	3.48	3.93
	♀	34	85.74±0.32	2.44	2.85
Tail.....	♂	49	103.18±0.64	4.48	4.34
	♀	30	100.13±0.82	4.49	4.50
Bill from nostril.....	♂	52	11.14±0.07	0.55	4.90
	♀	35	11.07±0.08	0.45	4.11
Tarsus.....	♂	52	31.61±0.16	1.17	3.70
	♀	35	30.84±0.16	0.96	3.10
Hind toe with claw....	♂	52	22.60±0.14	1.05	4.63
	♀	35	22.67±0.20	1.17	5.16
IMMATURES					
Wing.....	♂	11	84.40±0.96	3.19	3.78
	♀	15	84.49±0.68	2.25	2.66
Tail.....	♂	9	99.00±1.61	4.83	4.88
	♀	15	99.80±0.89	3.45	4.36
Bill from nostril.....	♂	11	10.68±0.16	0.52	4.92
	♀	15	10.57±0.11	0.42	3.97
Tarsus.....	♂	11	30.52±0.29	0.97	3.17
	♀	15	30.65±0.18	0.71	2.31
Hind toe with claw....	♂	11	22.84±0.19	0.62	2.72
	♀	15	22.10±0.15	0.60	2.71

Diagnosis.—Similar to *P. o. ocai* and *P. o. brunnescens* but flanks browner (less gray) than either. Under tail coverts paler than in *P. o. ocai*. This race has narrowest pectoral band of races having a well-developed band. For comparisons of size see figures 7 and 8 and table 12.

Distribution.—The Sierra Madre del Sur of Guerrero, at least west of Chilpancingo. Not known east of Chilpancingo.

Specimens examined.—Total, 121 (♂♂, 53; ♀♀, 37; ♂♂ im., 4; ♀♀ im., 5; ♂♂ juv., 9; ♀♀ juv., 10; unsexed, 3).

GUERRERO: Omilteme, 11 ♂♂, 4 ♀♀, 1 ♀ im., 1 ♂ juv., 3 ♀ juv. (MVZ); 1 ♂ (CNHM); 3 ♂♂, 1 ♀, 2 juv. sex? (USBS); 1 mi. E Omilteme, 7,400 ft., 1 ♂, 1 ♀ (MVZ); Cuapongo, 33 ♂♂, 31 ♀♀, 2 ♂♂ im., 4 ♀♀ im., 7 ♂♂ juv., 6 ♀♀ juv. (MVZ); 1 ♂, 1 ♀ (CNHM); mts. near Chilpancingo, 2 ♂♂, 2 ♂♂ im., 1 ♂ im., 1 ♀ juv. (MVZ); 1 ♂ (USBS).

Habitat.—At the type locality, at 7,000 feet, the dominant trees are pines, oaks, and madrones, with occasional palms and junipers intermixed. The towhees inhabit brushy cover along ravines and at the margin of the wood-

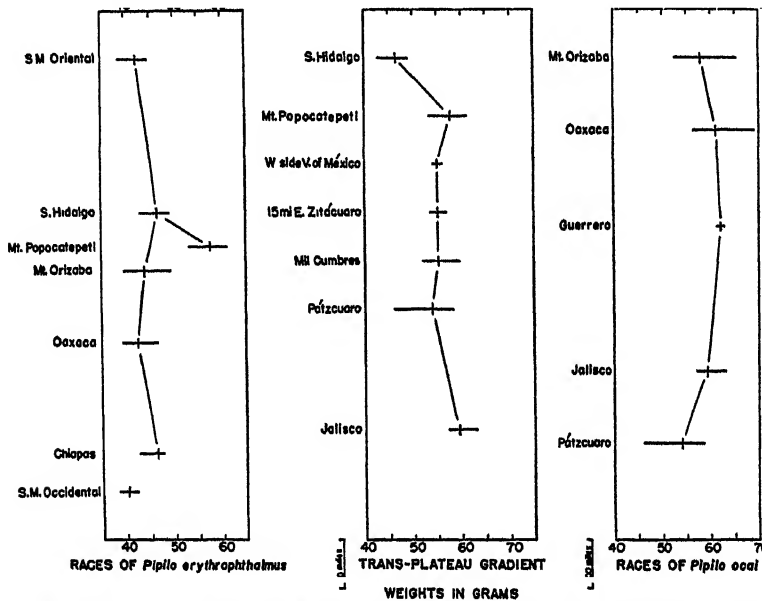


Fig. 9. Means and extremes of weights for some populations of Mexican towhees.

land. They are most abundant where the brush is dense and is about 10 to 12 feet high. Favorable habitat for *P. o. guerrerensis* near Omilteme extends down to about 6,400 feet. The birds do not occur below areas where both pines and oaks are found. Scrub oak and *Baccharis* sp. are two of the components of optimum cover for the birds at Omilteme (see pl. 14, fig. 2).

Discussion.—This is the only race of *P. ocai* which is not in contact in any way with *P. erythrophthalmus*. It is fully isolated in the highlands of the Sierra Madre del Sur.

The splendid series collected by W. W. Brown at and near the type locality has made possible the comparison of fall immatures and a mixed sample of adults plus undetectable spring immatures. Figures 7 and 8 include the statistical data for these series.

Pipilo ocai alticola (Salvin and Godman)

Chamaeospiza alticola Salvin and Godman (1889:381).

Pipilo torquatus alticola, Ridgway (1901:408).

Pipilo ocai alticola, van Rossem (1940:174).

Type.—No type designated. Type series from the Sierra Nevada de Colima, 10,500 feet, state of Colima, Mexico; collected by W. Lloyd and W. B. Richardson.

Diagnosis.—From *P. o. ocai*, *P. o. brunnescens*, and *P. o. guerrensis*, *alticola* is distinguished by lack of median frontal white line and reduced superciliary line. Both characters result from increase in melanins of head region as result of introduction of *erythrophthalmus* influence via trans-plateau gradient and the Cerro Viejo hybrid population. From *P. o. nigrescens*, *alticola* is separable by always having a completely white throat

TABLE 13
MEASUREMENTS OF *Pipilo ocai alticola*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	10	91.18±1.03	3.27	3.58
	♀	12	84.30±1.04	3.62	4.30
Tail.....	♂	10	102.64±0.96	3.04	3.00
	♀	12	93.44±1.52	5.26	5.63
Bill from nostril.....	♂	15	10.25±0.13	0.52	5.10
	♀	12	10.04±0.15	0.52	5.17
Bill depth.....	♂	10	8.77±0.10	0.33	3.72
Tarsus.....	♂	15	30.93±0.27	1.05	3.38
	♀	12	29.72±0.21	0.73	2.45
Hind toe with claw....	♂	15	22.61±0.20	0.79	3.50
	♀	12	22.15±0.38	1.33	6.01

and chestnut pileum. (See discussion on page 173 in reference to characters of *nigrescens*.) Figures 6, 7, 8, and 9 and table 13 contain data on size.

Distribution.—The mountainous region of western Jalisco from the vicinity of Mascota in the northwest, southeast at least to the Volcán de Colima. Probably extends eastward toward *P. o. nigrescens* in southeastern Jalisco.

Specimens examined.—Total, 31 (♂♂, 16; ♀♀, 13; juv., 2).

JALISCO: Sierra de Tapalpa, 15 mi. W Sayula, 7,450 ft., 4 ♂♂, 6 ♀♀, 1 ♂ juv., 1 ♀ juv. (MVZ); La Laguna, Sierra de Juanacatlán, 3 ♂♂, 4 ♀♀ (USBS); La Laguna, Mascota, Juanacatlán, 2 ♂♂, 1 ♀ (AMNH); 1 ♂ (USNM); Sierra Nevada, 1 ♂ (USBS); Los Masos, 5,800 ft., southern Jalisco, 4 ♂♂ (AMNH); La Pisagua, 1 ♂, 1 ♀ (AMNH); La Cumbre, Mascota, 1 ♀ (AMNH).

Habitat.—*P. o. alticola* is common above 6,500 feet in the Sierra de Tapalpa, where I observed it in August, 1946. The birds occur there in thickets composed of acacia, hawthorne, and *Baccharis*. The woodland at this locality is a pine-oak association (pl. 16, fig. 1). Two nests were found, one in an acacia and one in a hawthorne. Both nests were about four feet from the ground. One contained two nestlings, the other was empty.

Discussion.—*P. o. alticola* shows the effects of introgressive hybridization as described above (see *Diagnosis*). The effects are slight, but can logically be ascribed to no other source.

Pipilo ocai nigrescens (Salvin and Godman)*Chamaeospiza nigrescens* Salvin and Godman (1889:381).*Chamaeospiza torquata*, (not *Pipilo torquatus* Du Bus) Stone (1890:218), part.*Pipilo nigrescens*, Ridgway (1901:408).*Pipilo ocai nigrescens*, Blake and Ilanson (1942:548-549).TABLE 14
MEASUREMENTS OF *Pipilo ocai nigrescens*

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
CERRO SAN ANDRÉS AND PÁTZCUARO					
Wing.....	♂	20	89.14±0.33	1.50	1.67
	♀	14	84.16±0.67	2.52	3.00
Tail.....	♂	22	99.52±1.00	4.69	4.70
	♀	14	96.52±0.95	3.54	3.67
Bill from nostril.....	♂	19	10.14±0.09	0.40	3.95
	♀	14	10.13±0.12	0.45	4.50
Bill depth.....	♂	16	8.79±0.09	0.37	4.21
Tarsus.....	♂	21	30.68±0.18	0.81	2.65
	♀	14	29.75±0.26	0.99	3.34
Hind toe with claw....	♂	22	21.96±0.34	1.60	7.31
	♀	14	21.88±0.26	0.96	4.38
TANCÍTARO AND PATAMBÁN					
Wing.....	♂	14	87.90±0.56	2.09	2.38
	♀	6	82.82±0.60	1.47	1.77
Tail.....	♂	14	99.32±1.13	4.25	4.28
	♀	6	94.38±0.82	2.02	2.14
Bill from nostril.....	♂	14	10.58±0.11	0.43	4.09
	♀	6	9.95±0.20	0.49	4.94
Bill depth.....	♂	13	8.75±0.07	0.24	2.74
Tarsus.....	♂	13	30.96±0.24	0.86	2.79
	♀	6	29.67±0.43	1.04	3.51
Hind toe with claw....	♂	14	21.65±0.32	1.21	5.57
	♀	6	22.15±0.59	1.45	6.54

Type.—No type designated. Two specimens collected at Pátzcuaro, Michoacán, January, 1888, by F. DuCane Godman, formed the basis of the original description.

Diagnosis.—Because of the range of individual variation in this race, a simple diagnosis is difficult to make. Characters of population are discussed on page 173; see also figure 17. For comparisons of size see figures 5 and 6 and table 14.

From more stable populations of *P. ocai*, *P. o. nigrescens* differs in some-

times having black in throat, in lacking superciliary and median frontal stripes, in sometimes lacking chestnut in crown, in having rufescent flanks, and in sometimes having indications of tail spots. All these departures from other populations of *P. ocai* are due to effects of infiltration of *P. erythrophthalmus* genes via the *maculatus-vulcanorum-macronyx* clinal series.

Distribution.—As now known, the distribution is entirely within the state of Michoacán from Cerro San Andrés west to Mount Tancítaro.

Specimens examined.—Total, 63 (♂♂, 35; ♀♀, 20; sex?, 4; juv., 4).

TABLE 15
MEASUREMENTS OF CERRO VIEJO POPULATION

Part	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	♂	48	87.98±0.27	1.88	2.14
	♀	27	83.71±0.36	1.87	2.23
Tail.....	♂	48	99.66±0.50	3.41	3.43
	♀	27	93.85±0.55	2.88	3.10
Bill from nostril.....	♂	49	9.64±0.06	0.42	4.40
	♀	27	95.29±0.12	0.63	6.64
Tarsus.....	♂	49	29.27±0.12	0.82	2.80
	♀	28	28.70±0.15	0.79	2.74
Hind toe with claw....	♂	49	21.15±0.13	0.90	4.23
	♀	28	21.15±0.16	0.86	4.06

MICHOACÁN: Cerro San Andrés, 9,000 ft., 20 mi. SSW Morelia, 10 ♂♂, 8 ♀♀ (MVZ); 2 mi. SE Pátzcuaro, 7,700 ft., 5 ♂♂, 4 ♀♀, 1 juv., 5 mi. S. Pátzcuaro, 1 ♀ (GMS); Pátzcuaro, 1 ♂, 1 ♂ juv. (USBS); Quiroga, N side Lake Pátzcuaro, 1 ♂ (MVZ); 6 mi. W Quiroga, 1 ♂ (GMS); 5 mi. NW Tacámbaro, 6,900 ft., 1 ♂ (MVZ); Nahuatzín, 1 ♂ (USBS); Patambán, 3 ♂♂, 2 ♀♀, 2 sex? (USBS); Mount Tancítaro, 8 ♂♂, 3 ♀♀, 1 sex? (USBS); 4 ♂♂, 2 ♀♀, 2 sex?, 1 ♂ juv. (CNHM).

Habitat.—Near Pátzcuaro this race is abundant in brushy fence rows beneath, and at the margins of, pine woodland. On Cerro San Andrés, *nigrescens* is common from 8,000 feet to the summit at 11,900 feet. Preferred habitats are brushy fence rows or brushy borders at the margins of woodland areas. *Baccharis* is one of the principal components of the brush cover occupied by *P. o. nigrescens*.

Discussion.—*P. o. nigrescens* is one of the populations connecting *P. o. alticola* with *P. e. maculatus* across the plateau. It seems probable that other populations will be found between Tancítaro and the highlands of western Jalisco, where *P. o. alticola* occurs. On March 15, 1948, from the summit of Cerro Viejo at the northwestern side of Lake Chapala, I was able to see well-wooded ridges extending east from the vicinity of the Volcán de Colima. If these ridges carry suitable habitat, towhees should occur on them.

INTERSPECIFIC CONTACT AREAS

In four areas in Mexico, *Pipilo erythrophthalmus* and *Pipilo ocai* come into contact. On Cerro San Felipe, Oaxaca, the two live side by side without crossing. On Mount Orizaba, Puebla, they overlap in altitudinal distribution and occasionally interbreed. The population inhabiting Cerro Viejo, Jalisco, is the result of free hybridization between them, and the series of populations in the interval between southern Hidalgo and southwestern Jalisco, across the central highlands, presents characteristics which may be interpreted as both hybridization and intergradation.

THE OAXACA CONTACT

If two forms coexist in the same locality during the breeding season and, although no external barriers to interbreeding are present, do not interbreed, they are sympatric. Mayr (1942:120) proposes the following definition: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." If the preceding statements are accepted, it follows that if two forms can be proved to be sympatric they are good species.

Pipilo ocai brunnescens is a slight morphological differentiate of the collared towhee. From *P. o. ocai* of the Mount Orizaba region it is separable only by the slightly browner, less gray, flanks. *P. o. brunnescens* is an abundant bird in the uplands east of the city of Oaxaca, as on Cerro San Felipe and on Mount Zempoaltepec. It occurs on Cerro San Felipe from at least 8,400 feet to the summit at 10,200 feet.

Pipilo erythrophthalmus oaxacae differs morphologically from the *P. e. maculatus* of the Mount Orizaba region in having a buffier dorsum and in being of smaller size. As in *P. o. brunnescens* the differences, although constant, are not greater than average differences between other recognizable geographic races. *P. e. oaxacae* is more widely distributed than *P. o. brunnescens* because it descends to lower elevations. It occurs over a greater area in Oaxaca than does *P. o. brunnescens* and hence comes into contact with the latter wherever *brunnescens* occurs. *P. e. oaxacae* ranges from at least 6,700 feet to more than 9,000 feet on Cerro San Felipe; hence it overlaps altitudinally with *P. o. brunnescens* for more than 600 feet of vertical distance. On Cerro San Felipe the zone of overlap is about one-half to three-fourths of a mile horizontally. Because of the rugged terrain, the area of overlap is increased over that which would be present on a smooth slope.

The fact that the two forms have different tolerances to altitude indicates differing ecological requirements, or at least differing ecological tolerances. The fact that they overlap altitudinally suggests that their ecological tolerances also overlap.

Considering all races of *P. ocai*, it is apparent that the species is primarily a bird of the coniferous forest. It does not seem to be restricted by the conifers

per se, but its requirements are met by the higher altitudes and consequently it occupies the elevations demanded by most coniferous trees in Mexico. The niche of *P. ocai* within the coniferous association is very similar to that of *P. erythrophthalmus* at lower elevations, namely, in areas having dense thickets and brushy ground cover. At altitudes high enough for the bird's requirements, but where there is no coniferous forest, *P. ocai* occupies these dense thickets and the brushy ground cover. In many parts of the range of *P. ocai* the coniferous forest has been removed by man, but brushy fence rows have become established. *P. ocai* is more abundant in such fence rows than in areas of uncut coniferous forest with limited brushy cover.

P. erythrophthalmus varies more widely in its habitat requirements than does *P. ocai*. In general, however, it occupies lower elevations than *ocai*. On the slopes of Cerro San Felipe, *P. e. oaxacae* is especially abundant in fence rows and brushy cover of any type above 7,000 feet. It is as typical of the oak forest altitudes as *ocai* is typical of the coniferous forest altitudes. Similarly, the presence of *P. e. oaxacae* is determined not by the oaks but by the ecological conditions that favor both the oaks and the birds. Where the oak forest has been cut off and brushy fence rows have been established, the population density of *oaxacae* reaches its maximum.

The original forest cover on Cerro San Felipe between 7,000 and 9,000 feet was apparently a mixed evergreen and deciduous association with pines, firs, madrones, and oaks as dominant forms. There was probably a sharper ecological separation between *P. o. brunnescens* and *P. e. oaxacae* under primeval conditions, but even then they were certainly in contact along the borders of their respective habitats. It is likely that there was some overlap, for the vegetational demarcation is not, and probably was not, abrupt. The lack of a sharp line of separation between the optimum habitats for the two species is, of course, a reflection of the absence of a sharp line in physical conditions. The overlap in ecological factors permits the overlap of the birds.

Man's influence has somewhat altered primeval conditions, but the pattern of original vegetation can be inferred from the remaining uncut remnants. The result has been to increase the extent of optimum habitat for both *P. o. brunnescens* and *P. e. oaxacae* and to permit unrestricted intermingling of the two forms. Today they occur together in the numerous thickets, chaparral-covered hillsides, and thick fence rows, over a wide belt from 8,400 feet up to at least 9,000 feet on Cerro San Felipe. I have not personally investigated conditions on Mount Zempoaltepec, but it is likely that parallel conditions exist there.

On July 15 and 16, 1946, a preliminary survey of the towhees of Cerro San Felipe was conducted, and from March 31 to April 5, 1948, an intensive study was made in the vicinity of La Cumbre, a hamlet of a few huts at 9,000 feet altitude, 5 miles northeast of the summit of Cerro San Felipe, on the road that connects the city of Oaxaca with Ixtlán.

La Cumbre is a typical rural community of Mexico. The families living

in its five houses cultivate the hillsides, raising principally corn and squashes. Up the road about half a mile, where the descent toward Ixtlán begins, is another group of houses known as La Cima (The Summit), and downhill toward the city of Oaxaca are other small groups of houses. The entire slope is under cultivation from the floor of the valley at 6,000 feet to the summit at more than 9,000 feet. Between the fields and bordering the paths are heavy log fences. These soon acquire a surrounding thicket of shrubs and small trees that provide dense cover of the optimum type for *Pipilo*.

In 1948 we collected 18 *P. e. oaxacae* and 37 *P. o. brunnescens*. All were taken within a mile of La Cumbre, most of them within half a mile. All were taken in the zone of overlap where both species were abundant. The discrepancy in numbers collected is due more to the slight difference in wariness between them than to a marked difference in abundance.

Most of our collecting was done along fence rows (pl. 15, fig. 1) where both species were abundant and easily accessible. The two forms were found side by side repeatedly. There was no detectable segregation in the overlap area. Often we observed the two species within a few feet of one another and shot both from a single position. Some excerpts from my field notes will illustrate the situation. For April 1, 1948, they read as follows:

In early morning hunted along fence rows on ridge directly behind La Cumbre. In hunting down one path I first took a *P. e. oaxacae*. About 200 feet farther along in the same fence row, no change of vegetation, I took a *P. ocai*. Then, another few hundred feet, another *P. e. oaxacae*, and again another short distance, a second *P. ocai*! Later I shot a *P. e. oaxacae* and from the same spot shot at two *P. ocai* which got away. These were in the same fence row, only 50-75 feet apart. Childs reports that he saw both *erythrophthalmus* and *ocai* in the same bush.

On April 2, 1948, while watching a *P. e. oaxacae* singing from a small oak, I saw a *P. o. brunnescens* pass directly beneath, foraging slowly along the ground at the margin of a brushy thicket. Earlier the singing *oaxacae* had been foraging at the exact spot where the *brunnescens* passed.

This general pattern of observation was repeated daily by the three of us. Again and again we saw the two species within a few feet of one another, sharing the same thickets. We were unable to find any evidence of ecological separation which would prevent interbreeding. Both species were in breeding condition at the same time, as evidenced by their gonadal development.

The songs of the two forms on Cerro San Felipe were quite distinctive, and relatively little variation was noted. *P. e. oaxacae* was heard to sing only the usual "chip-chip-trrrr" or "chip-chip-cheee" of the Mexican races. *P. o. brunnescens* was heard to utter only the song which I have heard from most races of *ocai*, which sounds to me like "clee-o-weet-chip-trrrr." In comparison with the variations in song found in the hybrid zone on the western side of Mount Orizaba, Puebla, the songs of the birds on Cerro San Felipe were very constant.

A total of 64 specimens (21 *P. e. oaxacae* and 43 *P. o. brunnescens*) was collected in the overlap zone: 9 were taken in 1946, the remainder in 1948. I

examined each specimen in detail four times: once when it was collected, and three times since. Each time I carefully looked for evidence that would indicate that the two forms might occasionally interbreed. The evidence is negative. I have been unable to find the slightest hint of any crossing. None of the *P. e. oaxacae* has chestnut in the crown, a greenish tinge to the back, or brownish in the flanks. None of the *P. o. brunnescens* shows any reduction in the chestnut of the pileum, black shaft streaks in the back, or spots on wings or tail. The weights of the two are also well separated. Figure 9 indicates the relationships of this latter character. In contrast, the weights (fig. 11) as well as other characters show overlap on Mount Orizaba.

Because of the inherent limitations of negative evidence, it is impossible definitely to declare that these forms *never* interbreed in Oaxaca. However, it is apparent that, if they do cross occasionally, interbreeding is much less frequent than between the races *P. o. ocai* and *P. e. maculatus* on the western slope of Mount Orizaba. There, in 117 specimens, 19 hybrids were found, and, as previously indicated, the weights show some overlap in the females and closer approach in the males. If the frequency of crossing in Oaxaca were as great as on Mount Orizaba, we should expect to find 10 hybrids among the 64 specimens from the overlap zone and closer approach in weight.

Having thus eliminated ecological separation as an isolating factor and demonstrated sympatric existence for *P. e. oaxacae* and *P. o. brunnescens*, there can be no reasonable doubt that these two forms react as good species in Oaxaca.

THE ORIZABA CONTACT

The definition of the term "hybrid" has undergone nearly as much punishment as the definition of a "species." Mayr (1942:258) feels that interbreeding between categories of the rank of species or higher can unequivocally be called hybridization. He writes in part as follows:

Isolating mechanisms are not infallible, and, when they fail, forms will cross that had more or less diverged in their genetic make-up and taxonomic relationship. Such interbreeding is called hybridization. It is very difficult to define this term, or at least to delimit it against various forms of intraspecific interbreeding. The use of the term hybridization is undoubtedly justified if individuals of different families, genera, or good species interbreed.

Dobzhansky (1941:348) expresses the same idea:

The efficiency of physiological isolating mechanisms which hinder the exchange of genes between species inhabiting the same territory is sometimes incomplete. Their occasional breakdown leads to the appearance in nature of interspecific hybrids... Hybrids may appear as exceptional individuals, so that the limits of species are only slightly blurred, or the territory where the two species meet may be populated with "hybrid swarms."

Mayr (1942:259) applies the term "sympatric hybridization" to examples produced by a breakdown of the isolating mechanisms which prevent random mating, "in which an occasional hybrid is produced between two good species that coexist over wide parts of their ranges without mixing."

Chapin (1948) has recently described a situation in the paradise flycatchers

(*Terpsiphone*) of Africa which contains many similarities to the situation to be described in the towhees.

On Mount Orizaba in the state of Puebla, *P. o. ocai* and *P. e. maculatus* come into contact, although less extensively than do corresponding races of these species in Oaxaca. In contrast to the Oaxaca birds, the populations of Mount Orizaba produce occasional specimens which seem to fit the foregoing definition of a "sympatric hybrid."

It is of more than historical interest that the first specimen of the collared towhee to be made known to science, the type of Du Bus' *Pipilo torquata*, was a hybrid. This was recently pointed out by van Rossem (1940:173). Subsequently, other hybrid specimens contributed synonyms to either the spotted or collared species. Ridgway's names *complexus* and *submaculatus* were applied to intermediate specimens from Teziutlán, Puebla. It was the knowledge of the existence, and reasonable certainty of the significance, of these specimens which caused me to visit the western slope of Mount Orizaba in July, 1946, for a preliminary survey of the area.

On Mount Orizaba, as in Oaxaca, *P. erythrophthalmus* is tolerant of lower elevations than is *P. ocai*. On the western slope of Mount Orizaba, above the city of San Andrés de Chalchicomula, the forest cover has been removed up to about 10,000 feet altitude. In the brushy thickets below the edge of the remaining woodland, *P. e. maculatus* is abundant. The species was encountered from slightly above the level of Chalchicomula, at about 8,000 feet, to the present limit of clearing at 10,350 feet. At that level the mixed forest has been thinned but not completely removed.

P. o. ocai, like *P. o. brunnescens*, is typically a bird of the thickets at altitudes sufficient to permit the growth of a coniferous association. On Mount Orizaba, *P. o. ocai* is abundant from the present margin of the forest, at 10,000 feet, to at least 11,000 feet and probably as far as suitable habitat extends. At the lower edge of this range, *P. o. ocai* inhabits a narrow overlap zone with *P. e. maculatus*. Thus the two forms are ecologically separated for the most part, but because of the thinning of the trees by man their habitats have been made to overlap and the two forms have come to exist side by side as on Cerro San Felipe in Oaxaca. The zone of overlap on Mount Orizaba is somewhat narrower than that on Cerro San Felipe, but, as on Cerro San Felipe, there is no detectable segregation within the overlap zone. Both forms are found using the same thickets for cover and nesting. Chapin (1948:123) also found that the forest-clearing activities of man had been a factor in permitting ecologically separated species to come into closer contact.

On July 11 and 12, 1946, and from April 17 to 21, 1948, the overlap zone was investigated at a point 8 miles northeast of Chalchicomula, at 10,350 feet, on the southwestern shoulder of Mount Orizaba. This locality is directly up the slope above the village of San Martín Ojo de Agua.

Up to about 10,000 feet the forest has been removed and wheat is grown on the cleared slopes. Brush and small trees grow along ravines and on land

too uneven to plant. Between 10,000 and 10,500 feet the forest has been thinned and potatoes are cultivated in partly cleared fields. Above 10,500 feet the conifers are somewhat more dense and little of the land is under cultivation. Thus there is a belt of partly cleared land about half a mile wide

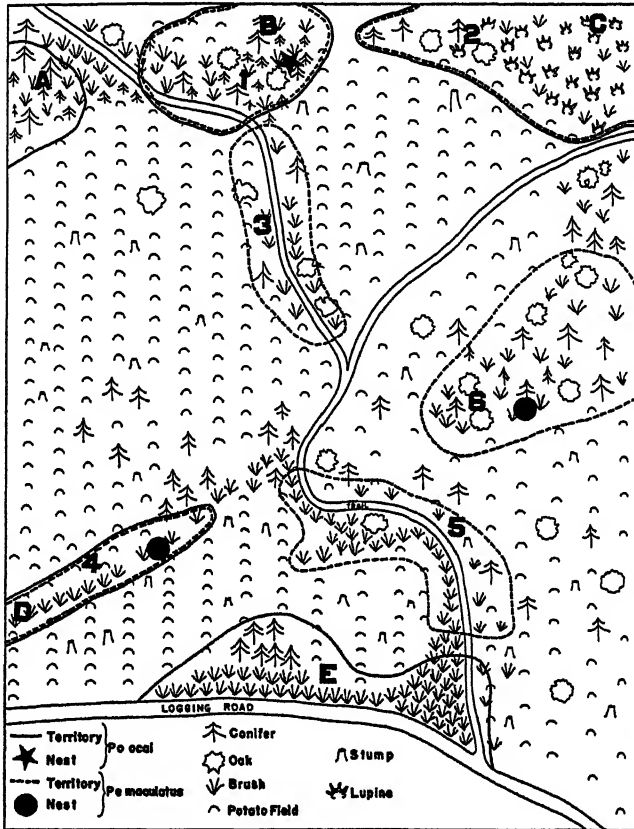


Fig. 10. Map of transect through zone of overlap between *Pipilo ocai ocai* and *P. erythrophthalmus maculatus*, 8 miles northeast of Chalchicomula, 10,350 feet, Puebla. Numbers (1-6) refer to pairs of *P. e. maculatus*; letters (A-E), pairs of *P. o. ocai*.

between the altitudes of 10,000 and 10,500 feet. This belt is at present characterized by fields with scattered trees remaining, brushy fence rows, and patches of thick brush and trees on areas unsuitable for cultivation or not yet cleared. The result is a habitat situation containing the necessary elements to permit the coexistence of *P. o. ocai* and *P. e. maculatus*. Both forms are abundant throughout the overlap zone. In 1946 I took 8 specimens in two hours; in 1948, two collectors obtained 72 specimens in four collecting days. The two species were the most abundant birds in the region, with the possible exception of *Junco phaeonotus*.

The two forms occurred side by side exactly as described on Cerro San Felipe. My notes for April 18, 1948, read as follows: "A pair of *P. ocai*, foraging along a brushy strip between fields. A male *maculatus* flew up to a small oak 50 feet from the *ocai* and from perch 15 feet up, sang. The pair of *ocai* came to the same thicket where the *maculatus* was and the male *maculatus*, which had been singing, flew down into the thicket near the pair of *ocai*." On the same date another pair of *maculatus* was observed carrying nesting material less than 75 feet from a singing *P. ocai*. This pattern of observation was repeated many times. We often saw both species in the same thicket, often within 5 or 10 feet of one another.

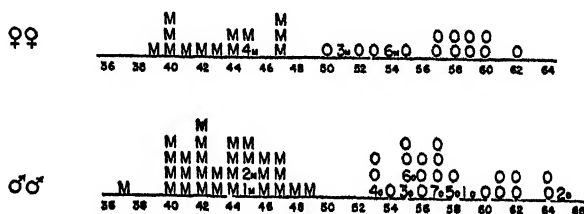


Fig. 11. Weight distribution of towhees from hybrid area on western slope of Mount Orizaba, 8 miles northeast of Chalehicomula, Puebla. 0 = *Pipilo ocai ocai*; M = *Pipilo erythrophthalmus maculatus*; numbers refer to hybrids shown in fig. 12 (weight not known for *P. e. maculatus* hybrid no. 5).

In 1948 I made a transect study through the overlap zone. The area chosen lay across a typical assortment of habitats. This area was 1,100 × 850 feet, with the long axis running east and west, parallel to the slope. Figure 10 is the map of this transect, showing the interdigitation of *ocai* and *maculatus* territories.

The five pairs of *maculatus* and four pairs of *ocai* found within the transect contained no mixed pairs. Two male *ocai* taken in the transect showed some evidence of mixed heritage. Otherwise, the birds of the transect behaved as good sympatric species.

The nests of two pairs of *maculatus* and one of *ocai* were found within the transect. The *ocai* nest and one of the *maculatus* nests contained two eggs each. The other *maculatus* nest held a single nestling less than a week old. The nest structure of the two species appeared basically the same. The nests all measured 75 mm. in interior diameter. The *ocai* nest was placed 8 feet up, in the branches of a small fir (*Abies religiosa*). One *maculatus* nest was placed 4 feet from the ground in the center of a bushy *Baccharis conferta*. The other was located 3 feet up, in a dense, shrubby *Eupatorium glabratum*.

The eggs of *P. o. ocai* are very similar in pattern and color to those of *P. e. maculatus*. The eggs of *ocai* have a faint bluish cast to the ground color; those of *maculatus* are white. The spotting of the *maculatus* eggs is more sharply defined and somewhat darker. The *ocai* eggs measure 26.2 × 18.9 mm.

and 24.6×18.6 mm. The *maculatus* eggs measure 25.7×18.7 mm. and 24.9×18.2 mm. The eggs of the two species are about the same size in spite of the discrepancy in size between the adult birds. Chapin (1948:123) noted that the nests and eggs of hybridizing species of the genus *Terpsiphone* are also very similar.

The song patterns of the two forms are basically similar, although each is readily distinguished from the other. The usual *maculatus* song is roughly syllabified as "chip-chip-trrr," two sharp notes followed by a trill. The trill may be a rapid buzz or slow and somewhat musical. Numerous variations are heard, however. One bird first sang the "chip-chip-trrr" pattern for several minutes, then switched to what was transcribed as "clert-weet-weet-chip-trrr." Another *maculatus* added a sharp "breet" note on the end of the usual song. The male of pair number 3 of the transect sang the usual "chip-chip-trrr" at intervals all day. One evening he was heard to utter a low, insect-like song which sounded like "zit-zit-zeeee-zit-zit."

The songs of *P. ocai* were also extremely variable. One pattern often heard sounded to me like "clee-o-weet-chip-trrr." The first male collected in area C, which showed evidence of mixed heritage, sang "wheer-tseet-tseet-trrrr" with a high-pitched, sibilant quality. The second *ocai* from area C, which also carried some *maculatus* characters, sang four different songs in fifteen minutes. Usually one song was repeated for several minutes, then a new one was uttered. The songs were transcribed "treee-chit-chit-chit; chit-chit-chit-chit; chree-tsit-tsit-trrr; chit-chit-chit-zeeer."

These examples serve to illustrate the great variation in song within each of the two forms, and the similarity in general pattern and in quality of song between the two forms. It is impossible to be certain whether the great variation in song is the result of occasional interbreeding; it may be, regardless of cause, a permissive factor favoring crossing. At least I doubt whether differences in song on Mount Orizaba are of importance in preventing the establishment of mixed pairs. On Cerro San Felipe there is noticeably less variation within, and more consistent difference between, the songs of the two species. *P. o. brunnescens* was heard to utter only the "clee-o-weet-chip-trrr" song and *P. e. oaxacae* was heard most often singing "chip-chip-trrr" with relatively little variation.

The call notes of the two forms are even more similar than the songs. Only after rather long experience was I able to distinguish between them with certainty. The call of both may be syllabified as "zhree" or "jor-ee." The call of *P. e. maculatus* is usually of the more drawn-out "jor-ee" type; that of *ocai* is sharper and shorter.

Chapin (1948:123) reports the calls and songs of two hybridizing species of *Terpsiphone* to be extremely similar.

I have been unable to detect significant differences in habits between *ocai* and *erythrophthalmus* which would tend to maintain segregation. They forage in similar places and in identical fashion. The habit of scratching vigorously

with both feet to uncover food items is as typical of *ocai* as of *erythrophthalmus*. In all other observed mannerisms the two also seem similar.

In summary, it is apparent that on the western slope of Mount Orizaba, *P. o. ocai* and *P. c. maculatus*, which are ecologically separated for the most part, come into contact at the margins of their respective habitats. The isolation which tends to keep truly sympatric species separate is not sufficiently complete to maintain strict segregation between the two forms, with the result that occasional mixed pairs are formed which give rise to hybrids.

I have examined 109 adult specimens of *P. o. ocai* and *P. c. maculatus* from the area between the town of Chalchicomula and Mount Orizaba. This includes 87 adults (48 *ocai* and 39 *maculatus*) from the overlap zone 8 miles northeast of Chalchicomula. Of the 109 specimens, 13 show evidence of hybridization with the other species; 12 of these were collected by myself or companions in the overlap zone. Each individual showing evidence of mixed ancestry is predominantly one species or the other: 6 are predominantly *maculatus*, 7 principally *ocai*. The synoptic descriptions of the 13 birds follow. Only the characters which differ from those of the species which they most resemble are described. The first 6 are predominantly *P. c. maculatus*.

1. Adult male, April 20, 1948. Broad chestnut tips and edges to crown feathers.

2. Adult male, April 18, 1948. Narrow chestnut edges to crown feathers.

3. Adult female, July 12, 1946. Broad chestnut tips to crown feathers so that crown appears about one-half chestnut. Throat mostly white with a broad white band down the center and white malar stripes. Tail and back spots reduced. Flank feathers tipped with olive. This bird had an egg in the oviduct nearly ready for laying.

4. Adult female, July 12, 1946. Crown suffused with chestnut. Flanks faintly tipped with olive.

5. Immature male, April 23, 1893. Crown feathers tipped and edged with bright chestnut. White throat spot. Olive-tipped flanks.

6. Female, April 17, 1948. Crown feathers tipped with chestnut.

The following 7 are predominantly *ocai*:

1. Adult male, April 18, 1948. Superciliary clouded with black. Throat white in center with white malar stripes separated by a solid black line; median frontal stripe absent. This is the first bird from area C of the transect; its song was described on page 159.

2. Adult male, April 20, 1948. Rectrices with white tips 2-3 mm. wide. Middle wing coverts faintly spotted.

3. Adult male, April 20, 1948. Bend of wing white, middle coverts distinctly spotted with white. Back color gray green rather than bright olive green as in *ocai*. Tail likewise suffused with blackish.

4. Adult male, April 20, 1948. Black stripes separating white of throat from white of malar region. Three outer rectrices with whitish tips. This is the second bird from area C of the transect; its four songs are described on page 159.

5. Adult male, April 18, 1948. Chestnut of crown suffused with black; size of chestnut patch reduced by black marginal areas. Superciliary suffused with black; median frontal line reduced. Nape heavily streaked with black; throat streaked with black laterally.

6. Adult male, April 19, 1948. Throat with only median area and faint malar stripes white; median frontal line absent. Superciliary greatly reduced. Median wing coverts with well-marked light spots.

7. Adult male, April 18, 1948. Bend of wing white; middle wing coverts distinctly spotted with white; greater wing coverts faintly tipped with white. Two outer rectrices tipped with white spot 1-3 mm. wide. Back gray green, not olive green as in *ocai*.

Besides these 13 complete specimens I have the three outer rectrices of a bird which was principally an *ocai*, but unfortunately was destroyed. These three feathers have the broadest white spots of any basically *ocai* bird I have examined. The entire distal margin of each feather is white for about 5 mm., but the whitish area does not fade out until 15 mm. from the tip on the two outermost feathers.

The other hybrids which have been described have mostly been named. The first of these was *Pipilo torquata* Du Bus (1847:105). The type was recently examined by van Rossem and redescribed by him (1940:173). The type of *torquatus* is mostly *ocai* in characters with these exceptions: median frontal stripe absent; chestnut crown patch reduced by black tipping to crown feathers and increased width of lateral black margins; superciliary lines reduced; back heavily streaked with black; lateral rectrices with a 12 mm. spot of white on inner webs, next pair with white tips.

Two intermediate specimens from Teziutlán, Puebla, were named by Ridgway (1886b:332). The original descriptions were very brief, but in a later paper (1886a:146-147) the birds were described in great detail so that a satisfactory analysis may be made of them.

Pipilo submaculatus was described from a female taken in November, 1884, at Teziutlán, Puebla. This bird is dominantly *maculatus* except for the following characters: back spotting greatly reduced, but faintly visible on lateral scapulars; wing spotting reduced; tail spotting reduced.

Pipilo complexus was based on a male, also taken at Teziutlán, in November, 1884. This specimen is so near the precise intermediate point between *P. o. ocai* and *P. e. maculatus* that it may represent an example of the F_1 generation. This bird has the following characters: a rufous patch on the crown which is suffused with black; reduced superciliary lines; white throat patch smaller than in *ocai*; back olive green with black shaft streaks; back spotting reduced and yellow in color; wing spots also yellow; tail spots about half the average size for *P. e. maculatus*; flanks seemingly most like *maculatus* but not exactly so.

In his remarks concerning this specimen Ridgway considers only the green-tailed towhee (*Pipilo chlorurus*) and "*Pipilo macronyx*" (= *P. e. vulcanorum* and (or) *P. e. macronyx* of the present paper). At the time the description of *P. complexus* was written, *Pipilo ocai* was placed in a separate genus, *Chamaeospiza* Selater (1858:304); hence it was not even considered in this connection.

The description of *Pipilo orizabae* Cox (1894:161) was actually written by Ridgway, as indicated in the introduction to the paper. The type came from Mount Orizaba, 11,000 feet, above Chalchicomula. This bird was sexed as a male. Nelson (1898:157) believed that the specimen was actually a

female. He considered it a synonym of *P. maculatus* Swainson. The original description is complete enough to yield evidence that the specimen is actually another hybrid, principally with *maculatus* characters. From *maculatus* it differs as follows: back nearly unicolor, being "plain grayish-brown"; white markings of back and wings reduced; throat spotted with white; size somewhat greater.

These four names, *torquatus*, *submaculatus*, *complexus*, and *orizabae*, are all that were applied to hybrids from Puebla. Other hybrid specimens are

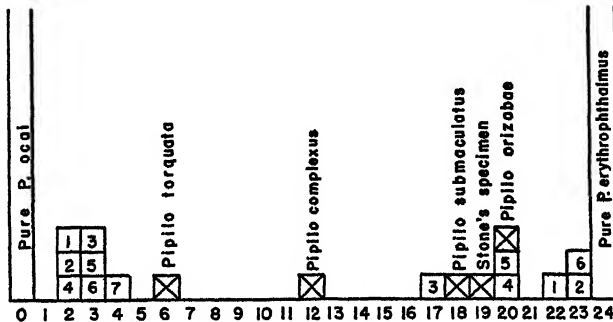


Fig. 12. Analysis of hybrids from Mount Orizaba and Teziutlán, Puebla. Numbers refer to specimens described on pp. 160-161.

known, however. Stone (1890:215) described three male *maculatus* from Mount Orizaba above Chalchicomula. One of these displays hybrid characteristics; the other two seem to fall within the normal range of variation for *P. e. maculatus* except for the presence of a "more or less prominent white spot on the throat." The most aberrant specimen differs from *maculatus* in the possession of a white throat spot and in that "the white streaks above are restricted entirely to the sides of the back, and are faintly tinged with yellow, as is also the case with the spots on the wing coverts, some of the latter being also narrowly edged with black. This specimen has a distinct white line from the bill to the eye." The white spots of the tail are reduced, the spot on the outer rectrix being but 15 mm. long.

Of the 117 specimens of which we have knowledge, 19 show evidence of mixed parentage. Thus, approximately 16 per cent of the specimens are the result of sympatric hybridization.

The hybrid specimens have been analyzed with relation to the pure types of the parental species by the method explained on pages 111-113. Figure 12 illustrates the distribution of intermediate specimens from Puebla. This graph is comparable to those illustrating the population characteristics of the Cerro Viejo hybrid population (fig. 15) and the clinal series of populations between the Valley of Mexico and Jalisco (fig. 18). The evaluation of characters from written descriptions is difficult, but the quantitative categories into which the characters have been divided are sufficiently large to make it possible.

As previously noted, *Pipilo complexus* is very close to being an exact phenotypic intermediate between *P. o. ocai* and *P. c. maculatus*. Since its position at the halfway point is dependent upon a summation of its characters, it is proper to examine each character separately. From Ridgway's description I evaluate every character at the exact midpoint, giving each a value of "2" on the 0-4 scale described on page 112. The flank color seems to weight the scale in favor of *maculatus*, but it is my experience that the rufous color of *maculatus* is dominant over the olive-brown color of *ocai*. This is indicated by the manner of distribution of this character in the Cerro Viejo hybrids (p. 166). I am uncertain about the correct value to ascribe to the flanks described by Ridgway as "paler rufous (almost buff)," and "pale ochraceous-rufous." A value of "3" for the flank color would move *P. complexus* one unit toward *maculatus*. This alters the picture very little; the bird is still close to an exact intermediate. In other characters I find no basis for seriously questioning the assignment of *P. complexus* to an exactly intermediate category. The type of *P. complexus* comes closest to what would be the expected phenotype of the F_1 from the crossing of a pure *ocai* with a pure *maculatus*. It could have been produced by some other combination of parents, but it is probable that it is the closest specimen to an F_1 individual that is known from the Puebla hybridization area.

The series of 9 specimens on the *maculatus* side of the midpoint vary among themselves from values of "17" units to "23" units. The variation is apparently due to the possible recombinations in the succeeding generations following a cross between pure types. For example, a bird with an index number of "18" could conceivably be the result of the cross between an individual like *P. complexus* with an index of "12" and a pure *maculatus* with a relative score of "24." An "18" bird could result from the pairing of a "17" and a "19" or any other combination with "18" as the midpoint value. This is assuming that all characteristics are controlled by equal numbers of genes and that the relative dominance of different characters is equal. Both assumptions are probably invalid for the most part. The genetic implications of variational patterns in hybrids are considered at greater length in the section dealing with the Cerro Viejo hybrids (pp. 165-168).

The foregoing remarks apply also to the hybrid series on the *ocai* side of the midpoint.

The application of a specific name to the collared towhee is a problem in nomenclature upon which the following analysis has bearing. The name *torquata* of Du Bus was founded upon a specimen of mixed ancestry. This was first noted by van Rossem (1940:173), who also presented the description of the type upon which my evaluation of its relative position was based. By my analysis the type of Du Bus' *P. torquata* is clearly a hybrid, but also clearly more *ocai*-like than *erythrophthalmus*-like. Does this fact make *torquata* referable to *ocai* and therefore available as a name for that population? I have decided against *torquata* for the following reason. The type of a

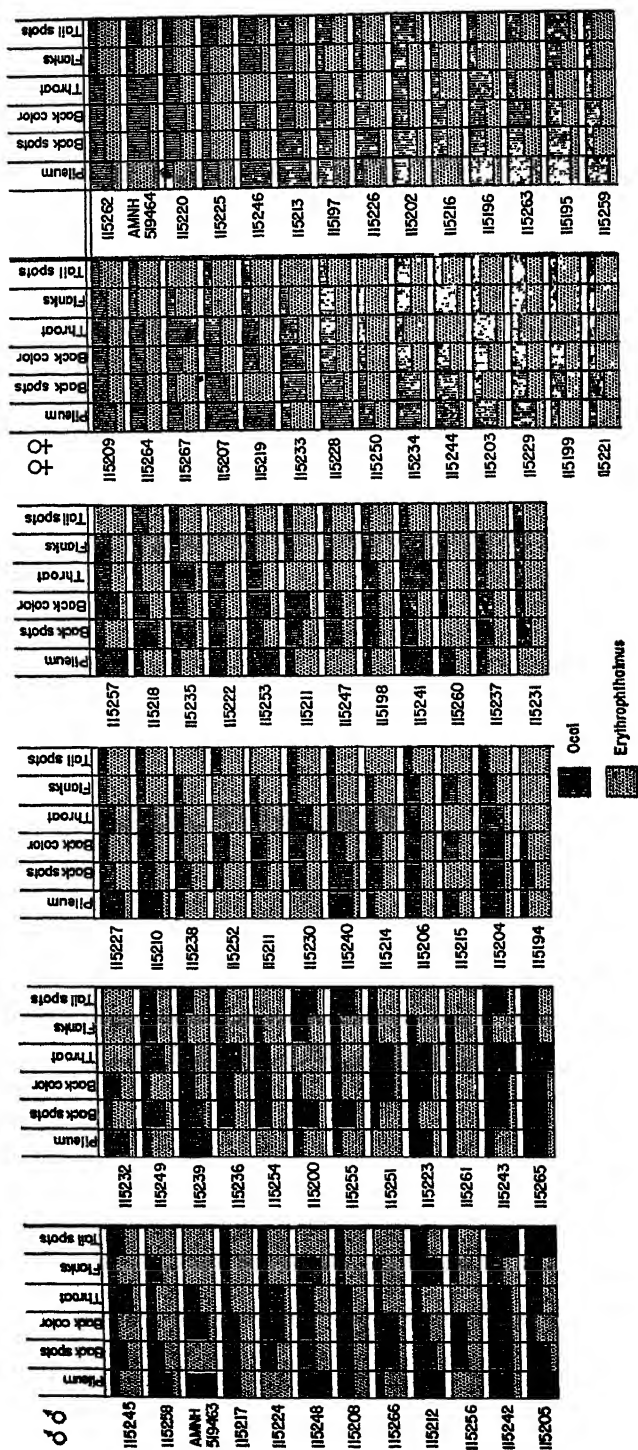


Fig. 13. Analysis of individuals in hybrid population of Cerro Viejo. Numbers refer to specimens in Museum of Vertebrate Zoölogy unless otherwise noted. See p. 166 for method of preparing graph.

species should theoretically be representative of a population. The type of *torquata* is representative only of itself. It is the only specimen out of 117 which has an index of "6," and is thus representative of less than 1 per cent of the population to which it would be applied. It is quite true that a type specimen is "typical of nothing," in the sense that in a normally variable population no two specimens are absolutely identical, but this is a special situation which falls outside the norm. For the present I prefer to use the name *ocai*, recognizing the decision as at least partly arbitrary. If a completely objective decision is possible, the publication of my data may bring it forth.

THE CERRO VIEJO HYBRID POPULATION

Mayr (1942:268) points out that "One of the striking phenomena of recently formed hybrid populations is their tremendous variation. Both parental types, as well as all the possible recombinations of the parental characters, may be found in the same effective breeding population." Dobzhansky (1941:81), in discussing the work of Baur and Lotsy on the plant genus *Antirrhinum*, notes that the F_2 of an interspecific cross "is enormously variable in all characteristics. Among hundreds of plants no two identical individuals can be found, and many siblings differ in a striking manner." Chapin (1948) describes a hybrid population in the musicapid genus *Terpsiphone* which is the result of the free interbreeding of two species at the site of a secondary contact. The hybrids show high variability because of recombinations of the parental characters.

The characters of the towhees inhabiting the summit of Cerro Viejo, Jalisco, display all these attributes of an interspecific hybrid population.

Three specimens showing hybrid characters were collected in the "Sierra de Cuyutlán" (= Cerro Viejo) by Dr. A. C. Buller in June, 1892. These birds were acquired by Rothschild, and eventually by the American Museum of Natural History. Notes taken on them for me by Mr. John Davis in 1947 led me to suppose that they were hybrids, and subsequent inspection of the specimens confirmed this. Cerro Viejo accordingly became one of the prime objectives of my field work in 1948.

Cerro Viejo is on the northwestern shore of Lake Chapala, about 22 miles south of Guadalajara, Jalisco. The mountain rises abruptly from the desert plateau at about 5,000 feet, and reaches a height of 9,700 feet. From a distance it appears barren and treeless, but the northern slope is thickly clothed with large trees and dense brush. The dominant trees are oaks and madrones (*Arbutus*). Dense thickets of a large woody *Salvia* (pl. 16, fig. 2) provide the principal towhee cover. Native woodcutters told me that a few pines grew on the mountain, but we did not find them. The area habitable by towhees was estimated to be 15 square miles or less. The birds were exceptionally abundant, being the commonest species present. In four collecting days, three collectors obtained 76 specimens.

Cerro Viejo was ascended from the village of Cuyutlán on the northern

side, and camp was established near the summit where water was available. Collecting was carried on from March 12 to March 16, 1948. This was during the breeding season and the birds were in full song. Songs were varied, and some were transcribed "tseer-chip-chip-chip; eer-tschip-tschip-tschip; eer-treeeee; chip-cher-cheeee" (= "Drink-your-tea" song of *P. e. erythrophthalmus*).

The call note was the usual "zhree," and many were heard to give the loud sibilant "tseer" note, which in other areas I have heard only from *P. ocai*. The "tseer" note of the Cerro Viejo birds was rough, however, not a pure, whistled note as in *P. o. alticola*.

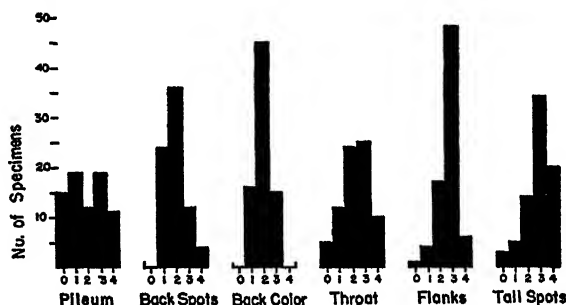


Fig. 14. Analysis of six primary characters in Cerro Viejo hybrid population. 0 = character as in pure *Pipilo ocai*; 4 = character as in pure *P. erythrophthalmus*.

No evidence of any type of segregation or preferential mating was discovered. The population is a freely interbreeding one.

The characters of the specimens collected on Cerro Viejo are presented in text figures 13 and 14. The method of character analysis used is that described on pp. 111-113. Figure 13 presents a synoptic description of 76 specimens (74 collected in 1948, 2 collected by Buller in 1892) from Cerro Viejo. The graphic patterns yield a picture of the characters of the entire population in terms of *ocai*-ness and *erythrophthalmus*-ness. By reading horizontally in figure 13, the characters of each specimen can be analyzed. By reading vertically, the distribution of each character in the population can be noted. Each of the six primary characters (see p. 112) is analyzed on the basis of five gradations of amount of expression. The arrangement of the specimens in figure 13 is entirely at random; they are not in the order of any one character.

Figure 15 shows the distribution of the summation of the characters of the population. This graph is derived from figure 13 simply by adding the number of *erythrophthalmus* units for each specimen and plotting the figures thus obtained on a 0 to 24 scale. This gives a single number for each specimen which expresses the sum of the characters of that specimen. For example, the first male in figure 13 has a pileum of "3" units, back spotting of "2," back color of "3," throat "1," flanks "3," and tail spots of "2." These add up to

"14" units; so this individual is entered at the "14" mark in figure 15. By this method the population average is found to be "13.7" on the 0 to 24 scale. Since "12" would be an exactly intermediate value, the population is seen to have an average complexion slightly to the *erythrophthalmus* side of the center.

Figure 14 shows the distribution of each of the six primary characters in the Cerro Viejo population. It will be seen that the characteristics of pileum, back spotting, back color, and throat are approximately neutral in their effect on the average for the total population illustrated in figure 15. Both flank color and tail spotting are skewed toward the *erythrophthalmus* side, however. It is due to the two latter characters that the curves of figure 15

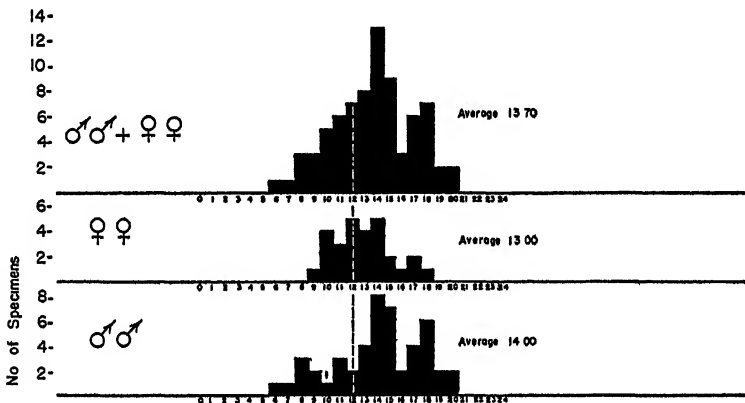


Fig. 15. Summation of characters in Cerro Viejo hybrid population.

are shifted toward *erythrophthalmus*. If the population were truly more *erythrophthalmus*-like than *ocai*-like, it would seem that all characters should show a tendency to be skewed toward *erythrophthalmus*. The fact that only two out of six do so leads one to suspect that the expression of flank color and tail spotting of the *erythrophthalmus* type may be dominant over the *ocai* type. Another explanation is that I may have been unable to evaluate these characters correctly and that I gave more weight to the *erythrophthalmus* type of coloration. It is apparent from an examination of the series, however, that all but one bird show some indication of the rufous color of *erythrophthalmus* in the flanks and that only three lack any trace of white on the tail.

Two other possible explanations of the skewed curves might be suggested. First, if the original parental stocks contained more individuals of *erythrophthalmus* than of *ocai*, there would be a greater number of *erythrophthalmus* genes in the population and hence more expression of the characters of that stock. Second, the habitat appears to be optimum for *erythrophthalmus*, but not so for *ocai*. Any selection impinging upon the hybrid population might favor the *erythrophthalmus*-like individuals and tend to move the population characteristics toward that form.

The enormous variability of the Cerro Viejo hybrids can be appreciated when it is realized that the population is at least fifteen times more variable than a "pure," stable population of either of the parental types. This is indicated by the spread of the population shown in figure 15 which extends from a value of "6" to one of "20." The pure parental populations would occupy only the interval of one index number, *ocai* at "0" and *erythrophthalmus* at "24." Compare the spread of the Cerro Viejo population (fig. 15) with the comparable populations of the transplateau cline (fig. 18). The Cerro Viejo population is as variable as the entire series of populations from the western side of the Valley of Mexico (*P. e. macronyx*) to the Pátzcuaro population (*P. o. nigrescens*). It is interesting that the average of the Cerro Viejo population, 13.7 units, is nearly the same as the average of the Mil Cumbres population, which is the most nearly intermediate between the extremes of the transplateau cline. In effect, the transplateau cline is an elongate hybrid zone with a series of relatively stable populations (compared with Cerro Viejo) laid end to end. The Pátzcuaro population, with a spread of 12 units, approaches the degree of variability of the Cerro Viejo population, although it is skewed well toward *ocai*.

The obvious difference between the Cerro Viejo situation and the transplateau cline is a result of the different geographical relations of the two. Cerro Viejo is, in effect, an island receiving occasional immigrants which contribute to the genetic melting pot and act to maintain the high variability. The transplateau cline is a series of semi-isolated populations, between any two of which there is constant genetic interchange. Since the two parental populations are at opposite ends of the cline and are in contact with one another only through the series of intermediate populations, the genetic effect of each parental population is diluted in proportion to the distance from where it is "pure." This situation produces a gradient bridging the morphological gap between the two extremes. It is likely that if a large enough sample of the Cerro Viejo population were obtained, the gap from 0 to 24 would be found to be entirely bridged, as it is in the transplateau series.

A series of 8 representative hybrids from Cerro Viejo is shown in color on plate 12. These are paintings of actual specimens chosen to show the range of variability from "6" to "20."

From an examination of figure 13 it can be seen that no two specimens of the Cerro Viejo series are exactly alike. The same situation was found in the snapdragons of Baur and Lotsy (Dobzhansky, 1941) as a result of the F_2 of an interspecific cross. The high variability in the Cerro Viejo population is thus in accordance with known interspecific crosses.

It is not difficult to determine the origin of the *ocai* component of the Cerro Viejo population. The nearest population, *P. o. alticola*, is not more than 30 miles west of Cerro Viejo. From the summit of Cerro Viejo the pine-clad ridges of the Sierra de Tapalpa are clearly visible to the southwest. *P. o. alticola* is abundant in that range.

The origin of the *erythrophthalmus* component is not so simple to determine. It is doubtful that the population of *P. e. griseipygius*, isolated north of the Rio Santiago, would readily cross the extensive barrier of the Santiago and its associated lowlands. The only other possible source of *erythrophthalmus* stock is from the northeast. Although no localities between Cerro Viejo and central Guanajuato are known for *P. erythrophthalmus*, I have seen at least one mountain which from a distance appears even more likely to support a population of towhees than does Cerro Viejo. This mountain is about 70 miles northeast of Cerro Viejo and about 13 miles east of Tepatitlán, Jalisco. The mountain is oak-covered and was judged to be about 8,000 feet high. On Cerro Viejo we found towhees well below 8,000 feet. If a series of such islands of favorable habitat exists between Cerro Viejo and the populations of *erythrophthalmus* in Guanajuato, it would seem to be the most likely avenue for the introduction of the *erythrophthalmus* component of the Cerro Viejo hybrid population.

Since the foregoing analysis of the Cerro Viejo population was completed, a second hybrid population has been discovered on Cerro Tequila, 40 miles in an air line northwest of Cerro Viejo. Mr. J. R. Alcorn, collecting for the Museum of Natural History of the University of Kansas, obtained 4 hybrid towhees there on May 10 and 11, 1949. Descriptions of these 4 specimens from Cerro Tequila, 10,000 ft., 7 mi. S and 2 mi. W Tequila, Jalisco, are as follows:

1. Adult male, KU no. 27555. May 10, 1949. Testes enlarged, 9 mm. Pileum with posterior $\frac{3}{8}$ chestnut, anterior $\frac{1}{8}$ black (1); spotting of wings and back faintly yellow (2); back black admixed with greenish (2); throat black (4); flanks rufous with a faint tinge of olive (3); tail spots white but reduced (3). (The numbers in parentheses indicate unit values on the 0-4 scale of fig. 14.)

2. Immature male, KU no. 27558. May 11, 1949. Testes 1 mm. Molting. Juvenal plumage mostly replaced by first winter plumage, but approximately 10 per cent of the juvenal feathers remain. Posterior part of the pileum coming in chestnut; otherwise seemingly most like *erythrophthalmus*.

3. Sex? KU no. 27556. May 10, 1949. Molting. Approximately 75 per cent of plumage consists of juvenal feathers. Chestnut feathers coming into posterior part of pileum; wing and scapular spotting reduced; throat black except for light-colored juvenal feathers; flanks intermediate between *ocoi* and *erythrophthalmus*; tail spotting almost absent; only faint whitish spotting on the 2 outer rectrices.

4. Sex? KU no. 27557. May 11, 1949. In juvenal plumage with post-juvenal molt just beginning. Appears to be most like *erythrophthalmus*, but pileum color not determined in this plumage.

THE TRANSPATEAU GRADIENT

Reference to the map (fig. 16) will serve to locate the geographical positions of the series of populations to be considered. It is convenient to take up the problem of their variation from east to west, beginning with the stable population of *P. e. orientalis* in the Sierra Madre Oriental and progressing south to southern Hidalgo where *P. e. maculatus* occurs; thence to Mount Popocatepetl (*P. e. vulcanorum*), the western side of the Valley of Mexico, including the Volcán de Toluca (*P. e. macronyx*) and "15 mi. El Zitácuaro" (*P. e. macronyx*).

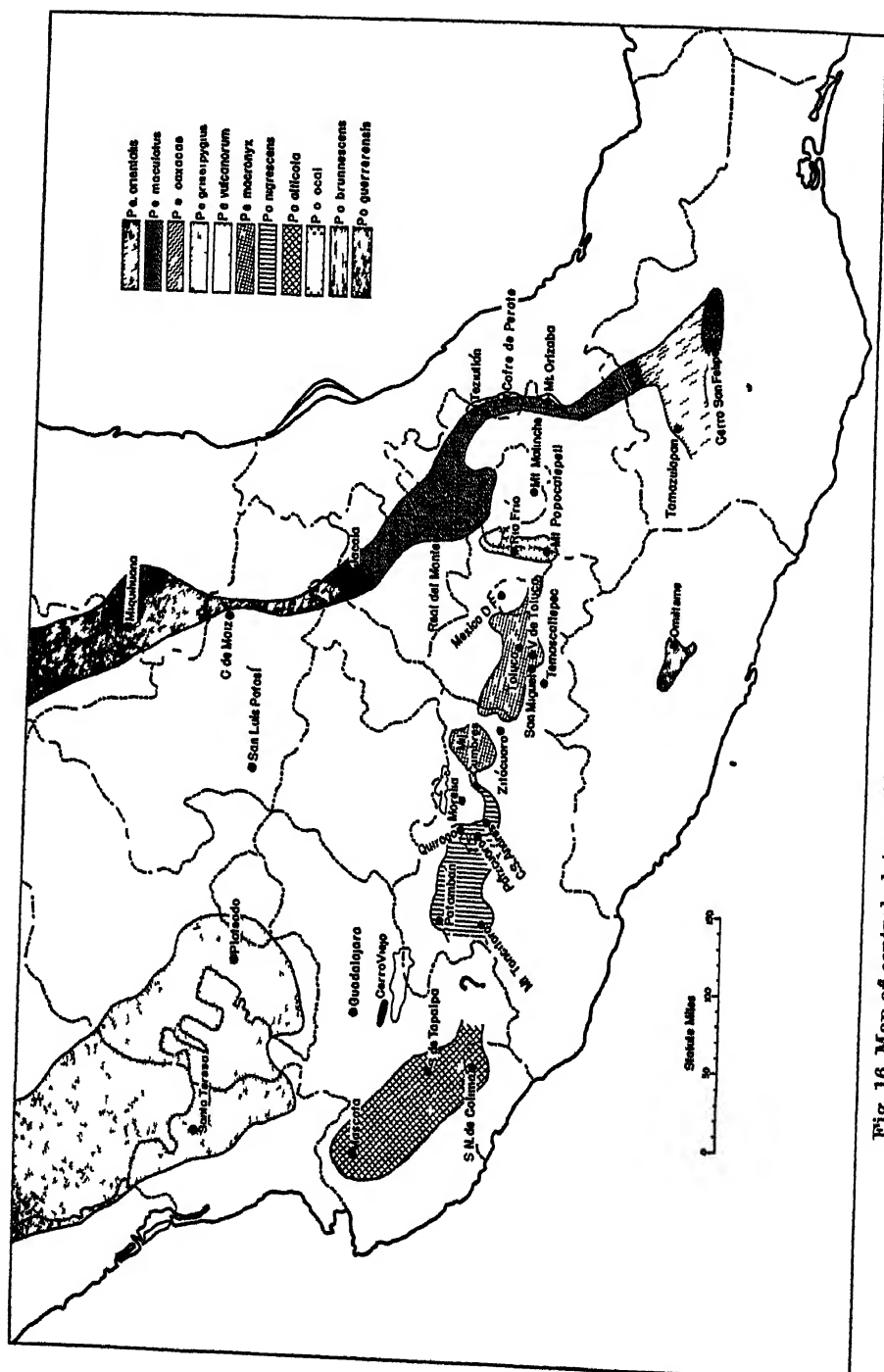


Fig. 16. Map of central plateau of Mexico showing principal localities mentioned.

Next is the population inhabiting the Sierra de Ozumatlán, or Mil Cumbres. This population is intermediate between *P. e. macronyx* and the population of the Pátzcuaro basin, *P. ocai nigrescens*. (The apparent nomenclatural impasse indicated by these trinomials will be discussed later, on pp. 175-176.) The towhees of the regions of Tancitaro and Patambán (*P. o. nigrescens*) are next considered, and finally the population of *P. o. alticola* in Jalisco.

The series of populations from southern Hidalgo to Jalisco has been analyzed in the same manner as the Cerro Viejo hybrids (see pp. 166-167). Figure 18 is the graph showing the summation of color characters of the series of transplateau populations. This graph is comparable to the analysis of the Cerro Viejo hybrids (fig. 15) and to that of the Mount Orizaba hybrids (fig. 12). Figure 17 is based on the analysis of each of the six primary characters in the transplateau populations. It is comparable to the analysis of the characters in the Cerro Viejo population (fig. 14).

The population of the Sierra Madre Oriental (*P. e. orientalis*) is a relatively stable one. All individuals of *P. e. orientalis* would fall at the index number "24" on the scale of figure 18. In geographical continuity with *P. e. orientalis* is the Hidalgo population, *P. e. maculatus*. The birds inhabiting southern Hidalgo (Sierra de Pachuca, El Chico, Real del Monte, Irolo, and San Agustín) are in contact to the north with *orientalis* and to the south with *P. e. vulcanorum*. The contact with *vulcanorum* is not a free one, but is only partial because of an area of low topography and resultant unfavorable habitat between the two races. Reference to figures 5 and 6 will show that the effect of *vulcanorum* on the linear dimensions of *maculatus* is to cause the *maculatus* dimensions to vary in the direction of the larger ones of *vulcanorum*. The apparent discrepancy in length of bill is due to the fact that the bill of *vulcanorum*, *macronyx*, and races of *ocai* is short and thick. This is indicated by the pattern of variation for depth of bill (fig. 6).

The color of *maculatus* is also affected by the genetic influence from *vulcanorum*. This is graphically indicated by figure 18. The birds of southern Hidalgo have an average summation of the six primary color characters of "22.4." This average is due to the *vulcanorum* influence causing back color and throat color to tend toward that of *vulcanorum*.

The distance between the Pachuca region of Hidalgo and Mount Popocatepetl is only 70 miles in an air line. The population of Mount Popocatepetl (*vulcanorum*) is larger and greener and has fewer dorsal spots than *maculatus*. Its average summation of characters (fig. 18) is "19.8." Across the southern end of the Valley of Mexico, 50 miles (average) in an air line from Popocatepetl, is the population herein called *P. e. macronyx* (= *virescens auctorum*). This population is greener than *vulcanorum* and has fewer dorsal spots, less white in the tail, more olive color in the flanks, and in general shows the effect of its geographic and genetic proximity to *P. ocai nigrescens*. The average of the summation in the population of the western side of the Valley of Mexico is "16.9."

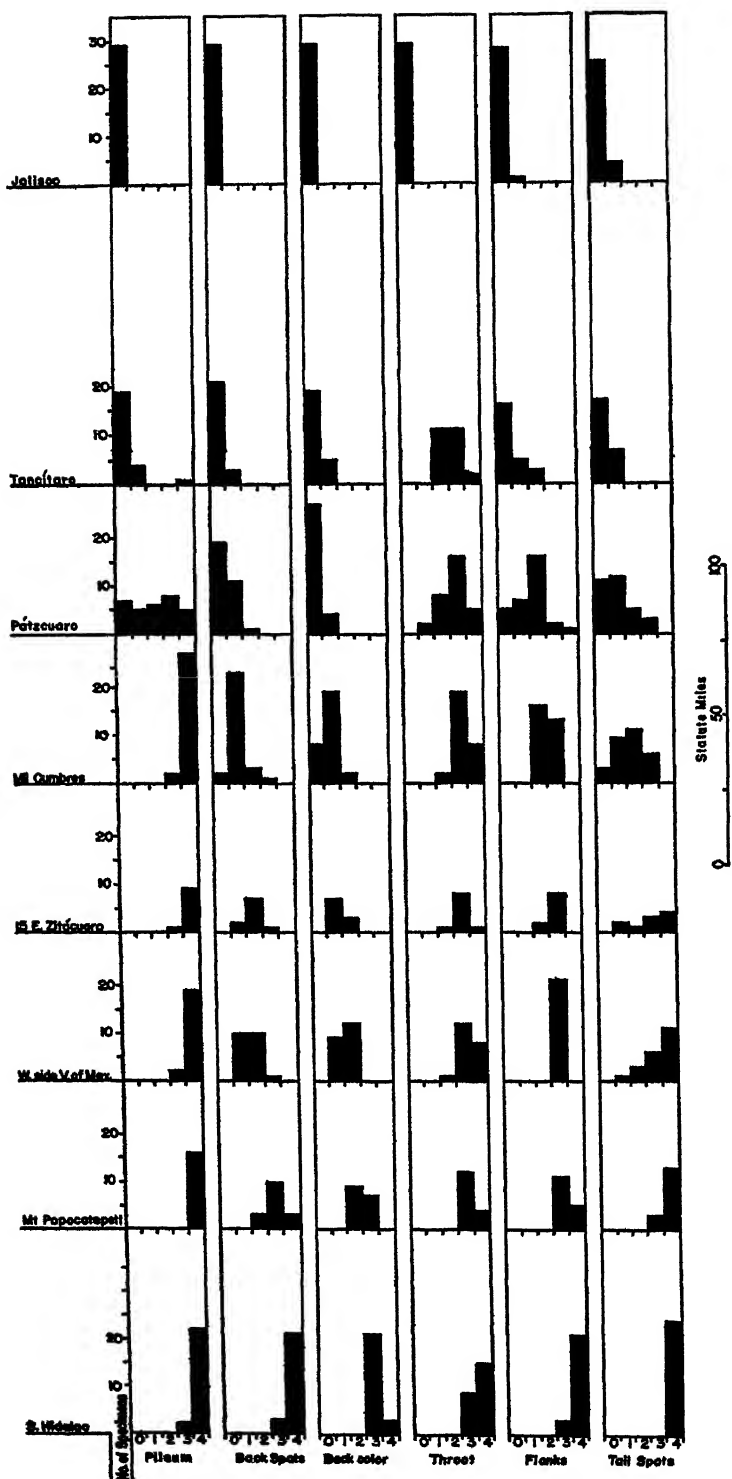


Fig. 17. Character distribution of populations of transplateau series. 0 = character as in pure *Pipilo ocai*; 4 = character as in pure *P. erythrophthalmus*.

Although no significant barrier intervenes between the population of the western side of the Valley of Mexico and the population at "15 mi. E Zitácuaro" on the Michoacán-México border, a slight shift in average characters is found in the 50-mile stretch, so that the latter population has an average of "15.8."

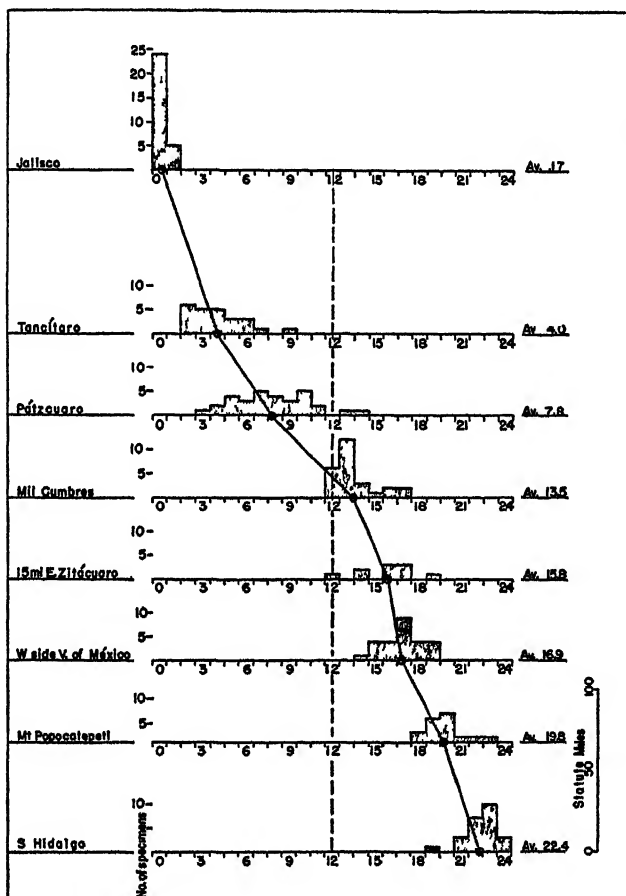


Fig. 18. Summation of color characters in populations of transplateau series.

A significant barrier, the Rio Tuxpan, prevents free exchange between the Mil Cumbres birds and those of "15 mi. E Zitácuaro." The Mil Cumbres population falls very close to the intermediate point with an average of "13.5." The Mil Cumbres population occupies the curious position of being the transitional population between what, for *practical* nomenclatural purposes, are considered herein to be two species. This point is discussed on pages 175-176.

Genetic exchange between the Mil Cumbres population and the birds of

the Pátzcuaro region is reduced by the narrow neck of suitable habitat connecting the two areas. The Pátzcuaro population is highly variable, but is strongly *ocai*-like in character, with an average of "7.8." In the Pátzcuaro birds the pileum is chestnut in a high percentage of individuals, and tail and back spots nearly disappear. The throat remains largely black and the flanks rufous, however. Back color is strongly *ocai* in type.

Only 50 miles west of Pátzcuaro, without an intervening barrier, the Tancítaro and Patambán birds show a still closer approach to *ocai*, with an average of "4.0." This is due to increasingly chestnut pileum color, greener dorsum, further reduction of wing and tail spots, and an increasing amount of olive in the flanks. Only the throat is as in *erythrophthalmus*, being mainly black.

The last 100-mile jump to the mountains of western Jalisco completes the gradient to "pure" *ocai*. Even in this population (*P. o. alticola*), however, there are indications of *erythrophthalmus* influence: 1 specimen has flecks of rufous in the flanks, and 4 have narrow white tips to the outer rectrices. All individuals of *alticola* lack the median frontal white line found in the other pure races of *ocai* (*P. o. ocai*, *brunnescens*, and *guerrerensis*). Moreover, the superciliary line is clouded with black, and the pectoral collar is relatively broad in *alticola*. All these conditions are apparently the result of an increase in the melanins of the head caused by the influx of *erythrophthalmus* genes via the transplateau gradient and the hybrid population on Cerro Viejo.

As shown in figure 17, the six primary characters display different geographic gradients across the transplateau region. Pileum color is strongly *erythrophthalmus* (black) in character until the Pátzcuaro region is reached. In that population every gradation of pileum type is found in approximately equal numbers, and the variability in that character is correspondingly high. Only 50 miles farther west, relative stability in pileum color is once more attained in the Tancítaro-Patambán population. In these birds, however, the shift to the *ocai* type (chestnut) has been made. All Jalisco birds seem to have the maximum expression of the *ocai* type of pileum.

Back spotting displays a smooth gradient from a maximum in Hidalgo, through gradually shifting values, to complete absence in Jalisco. This same clinal pattern of variation is found for back color.

Throat coloration has a pattern of variation all its own. It remains strongly *erythrophthalmus*-like through the Tancítaro-Patambán population, but shifts suddenly to the *ocai* type in Jalisco. The shift, however, is not so sudden as the graphic picture of figure 18 indicates: there is evidence that the amount of black in the head of *alticola* is greater than in the genetically untainted races of *ocai*.

Flank color shows a gradually shifting value from rufous to olive gray, but its gradient is similar in appearance to that of the pileum. As with pileum color, the maximum range of variation in flank color is found in the Pátzcuaro population.

Tail spotting shows a gradual shift from maximum in Hidalgo to near absence in Jalisco. As might be expected in a character which is highly variable even in a stable population, it shows great variability, especially in the central populations of the gradient.

As with any quantitative character expressed phenotypically as a graded series, these characters are undoubtedly controlled by a multiple-factor genetic system. The pattern of variation in the six primary characters yields some evidence on the relative number of factors controlling each character. The characters with a wide range of variation in most or all populations and with gradually shifting averages are probably controlled by a greater number of factors than those which have narrower limits of variation and sharper shifts of the average. For example, tail spotting is probably controlled by more genes than is pileum coloration, and back spots and back color by about the same number of genes.

If selection is assumed to be of no significance, the relative dominance of different characters may be inferred by the degree to which a character is able to penetrate into the populations of the other species. Thus the black throat and head of *erythrophthalmus* seem to show some degree of dominance over the head type of *ocoi*. These suggestions are only speculative, and will remain so until it is possible to test them by breeding experiments.

As suggested in discussing the Cerro Viejo hybrid population, the trans-plateau gradient is in effect an elongate hybrid zone with its semi-isolated populations reaching partial stability. Thus the series takes on the aspect of a chain of highly variable geographic races. The gradient is the result of the geographic relationships which operate to maintain the long, narrow belt of suitable habitat between two large areas occupied by the parental species. The effect of isolation by distance and of isolation by barrier both contribute to the character of the gradient. The parental populations at opposite ends of the series maintain the variability of the intermediate populations by the constant flow of genes into the terminal populations and thence through the series. The effect of the parental populations on any one of the intermediate populations is proportional to the degree of isolation, by distance or by barriers, between the two.

It is apparent that, although a well-marked gradient exists between the two parental populations at opposite ends of the series of connectant populations, the picture is not the same as the pattern of variation usually called "intergradation." The differences from a typical intergrading contact are the great variability of the intermediate populations and the extreme differences between the terminal forms. It could be argued that between any two adjacent populations there is a typical pattern of intergradation on the subspecific level and that there is thus a series of small steps bridging the seemingly enormous gap between the terminal forms. This is true, but it does not explain the extraordinary variation within the intermediate populations which follows the pattern of the hybrid population of Cerro Viejo.

I think that the most logical interpretation of this gradient population series is to consider it to represent an elongate hybrid zone, the geographically limited segments of which have attained a certain degree of stability and differ from one another by about the same amount, as do typical geographic races of one species.

Regardless of what the series is called, its effect is to link *Pipilo ocai* with *Pipilo erythrophthalmus* through a series of intermediate populations. This argues strongly for considering the two species to be conspecific. I do not do so, however, for the following reasons:

1. They are sympatric in Oaxaca.
2. They are mainly sympatric on Mount Orizaba, although hybrids are found there.
3. The Cerro Viejo population shows a pattern of variability similar to that of other interspecific hybrid populations.
4. The transplateau gradient, although it is composed of a clinal series of populations, is the result of secondary intergradation, not the primary type usually found between intergrading subspecies.

For nomenclatural convenience I therefore advocate that the populations east of a point 10 miles east of Morelia, Michoacán, be considered races of *Pipilo erythrophthalmus*, and those populations west of that point be included in *Pipilo ocai*. This must be recognized as a practical solution to the incompatibility of Linnaean nomenclature in this special situation and should not be regarded as a synopsis of the biological situation.

SUMMARY AND CONCLUSIONS

Pipilo maculatus, *Pipilo macronyx*, and *Pipilo erythrophthalmus* are considered to be conspecific. The name *Pipilo erythrophthalmus* has priority and hence becomes the specific name of the group.

The name *macronyx* Swainson is shown to apply to the same population to which *virescens* Hartlaub has long been applied. Hartlaub's name *virescens* becomes a synonym of *macronyx* Swainson. The population hitherto called *Pipilo macronyx macronyx* is left nameless and is herein named *Pipilo erythrophthalmus vulcanorum*.

Ten subspecies of *Pipilo erythrophthalmus* are considered. Nine of these occur wholly or in part in Mexico. Three are newly described: *P. e. orientalis*, *P. e. oaxacae*, and *P. e. vulcanorum*.

Five subspecies of *Pipilo ocai* are recognized. No new races are described and none is synonymized.

Two type localities are herein restricted: that of *P. e. macronyx*, to the western slope of the Volcán de Toluca, state of México; and that of *P. o. ocai*, to Las Vigas, state of Veracruz.

The results of four secondary contacts between races of *P. erythrophthalmus* and *P. ocai* are described.

1. In Oaxaca the two species exist sympatrically without interbreeding.
2. On Mount Orizaba the two species exist sympatrically but produce occasional hybrids.

3. On Cerro Viejo, Jalisco, a hybrid population between the two species shows enormous variability because of the recombination of the characters of the two parental species. No two specimens in the 77 examined are alike. A series of populations extending across the central highlands from southern Hidalgo to Jalisco connects the two species without a sharp morphological discontinuity. These populations are highly variable.

It was pointed out earlier in this study that if the theory of species formation through microevolution is correct, natural populations should be found which could be demonstrated to represent intermediate stages in the process. The best clue to the stage of species formation which a given form has reached is its reaction to its congeners when they come together after a period of isolation and differentiation. If differentiation between them has reached the species level, they will live side by side and maintain their reproductive isolation. If differentiation has not proceeded beyond the subspecific level, they will interbreed freely and any differences between them will be swamped out if all barriers are removed. Between these two extremes is a theoretically infinite number of possible degrees of reproductive response. These intermediate stages are characterized by the condition usually called hybridization or secondary intergradation, which occurs when two incompletely formed species come into secondary contact.

The four secondary contacts between *P. erythrophthalmus* and *P. ocai* provide tests of the degree to which reproductive isolation between them has been attained. The results of the contacts indicate that the degree of isolation between the two species is different in each of the four contact areas. The significance of these differences in interspecific reproductive response lies in their interpretation as indicating stages in the dynamic process of species formation from subspecific population units.

In Oaxaca the process of species formation has progressed to the species level, and reproductive isolation has been achieved. On Mount Orizaba the secondary contact between the two groups has resulted in a small amount of hybrid formation indicating partial but incomplete reproductive isolation. The two hybrid zones, or populations, of Cerro Viejo and of the transplateau region illustrate other degrees of isolation attained at the time the secondary junction was effected.

Time is not the only factor affecting the attainment of reproductive isolation. Mutation rate and selection pressure also affect the rate and hence the degree of differentiation. Thus different degrees of hybridization can arise as the result of secondary contacts between different populations of the same two forms, even though it may be assumed that the original dichotomy took place only once.

One possible explanation of the situation found today in the Mexican red-eyed towhees is the following. From a common ancestor the *ocai* and *erythrophthalmus* progenitors were isolated and differentiated during their isolation. *P. ocai* became adapted to boreal conditions, but *P. erythrophthalmus* adapted to lower altitudes and therefore was able to occupy a much larger range.

Changing climatic conditions, perhaps associated with Pleistocene glaciation and the cessation thereof, forced *P. ocai* to the tops of mountains in order to remain in its optimum habitat. It thus became represented by the series of relict allopatric populations now found in the Mexican highlands. *P. erythrophthalmus* reinvaded southern Mexico, and secondary contacts were established with the *ocai* populations which *erythrophthalmus* could reach. Perhaps the first point at which contact was reestablished was in the Pátzcuaro area where *ocai* was resident and to which *erythrophthalmus* penetrated. Reproductive isolation was not yet complete and a zone of hybridization was established. The genetic effect of this hybrid zone spread in both directions and the transplateau gradient came into existence. The series of populations along the gradient gradually achieved a degree of stability intermediate between a pure population and a hybrid swarm. This gradient permitted the penetration of genes by introgressive hybridization from each form into the other. Thus, when *erythrophthalmus* came into contact with *ocai* on Mount Orizaba and on Cerro Viejo, one of the two forms in each instance was already genetically tainted by the other. The *erythrophthalmus* of Mount Orizaba were tainted with *ocai* genes from the west via the transplateau gradient, and the *P. o. alticola* involved in the Cerro Viejo situation were already impure by virtue of the influx of *erythrophthalmus* genes from the east. The physiological barriers to interbreeding were thus weakened and proved entirely ineffective on Cerro Viejo. Occasionally they proved ineffective on Mount Orizaba. By the time the two forms came into contact in Oaxaca, reproductive isolation was complete and the effect of the transplateau gradient was so diluted by distance that they remained reproductively isolated.

This suggested history is highly speculative and is presented only as one possible explanation of the present situation. It should be apparent, however, that the four contact areas are not mutually exclusive but are related so far as the breakdown of reproductive isolation at one contact will affect the isolation value at another contact.

If all animals currently displayed the patterns of variation that have been described in the Mexican red-eyed towhees, it would be impossible ever to arrive at a species concept. It is fortunate, however, that a few examples of this type are available for study, for they present the natural proving grounds for the neo-Darwinian theory of species formation.

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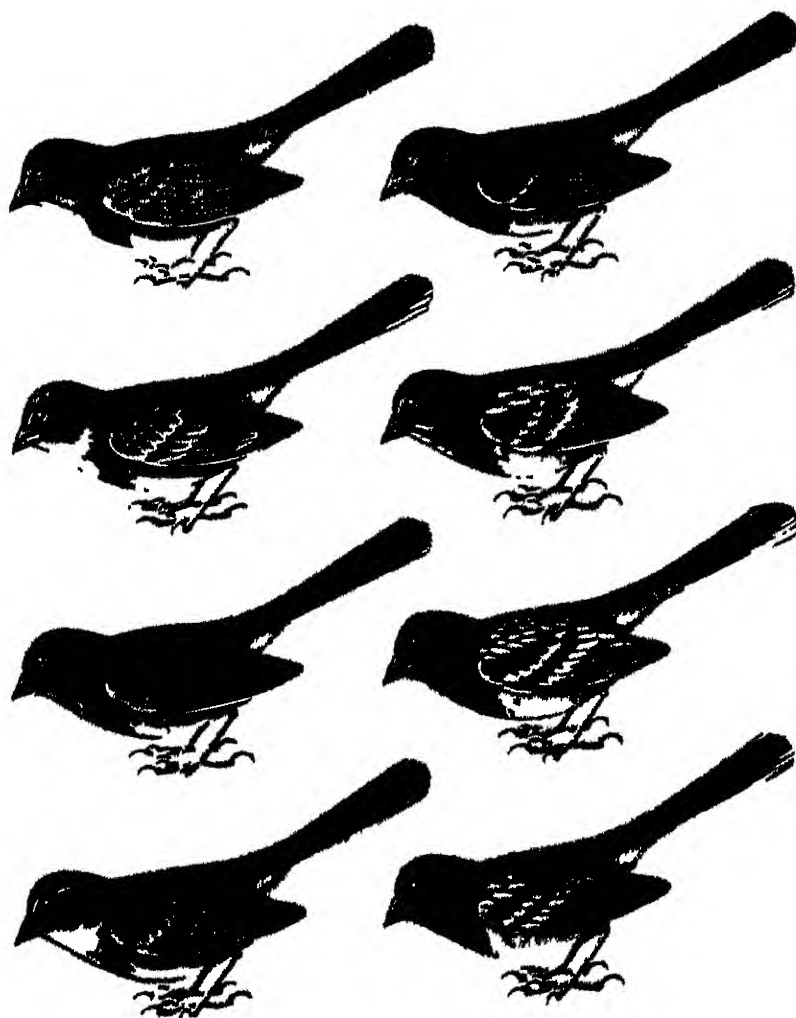
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PLATES

PLATE 12

Selected specimens from hybrid population of Cerro Viejo, Jalisco. These 8 specimens include the 2 extremes in available sample and some typical intermediate examples. Catalog numbers (Museum of Vertebrate Zoology) and index numbers (see fig. 15) showing degree of affinity to parental types are as follows:

Left column		Right column	
MVZ no.	Index no.	MVZ no.	Index no.
115242	6	115200	14
115241	8	115220	14
115212	8	115215	18
115243	9	115252	20



~R. STEBBINS~

PLATE 15

Fig. 1. Arid scrub at type locality of *Pipilo erythrophthalmus orientalis* 8 miles southeast of Galeman 6 000 feet. Nuevo Leon.

Fig. 2. Alpine meadow in pine-oak association 6 miles north of Pachuca 9 600 feet. Hidalgo. *Pipilo erythrophthalmus maculatus* occurs in brushy areas surrounding meadow. Dominant shrubs are *Juniperus* and *Baccharis*.



PLATE 11

Fig. 1 Habitat of *Pipilo erythrophthalmus maculatus* and *P. oear* in overlap zone on western slope of Mount Orizaba 8 miles north east of Chichicomula 10-50 feet Puebla

Fig. 2 Mixed pine oak woodland 1 mile east of Omiteme 7-100 feet Guerrero *Pipilo oear quercetensis* inhabits shrubby growth beneath trees



PLATE 15

Fig. 1. Typical fence row habitat at La Cumbre, 5 miles northeast of Cerro San Felipe, 9,000 feet, Oaxaca. Both *Pipilo erythrophthalmus oaxacae* and *P. oca brunneiceps* occupied brushy growth in foreground.

Fig. 2. Habitat of *Pipilo erythrophthalmus chiapensis*, 1 miles north west of San Cristóbal, 7,700 feet, Chiapas.



PLATE 16

Fig. 1 Mixed pine-oak forest in Sierra de Tapalpa, 15 miles west of Sayula, 7,450 feet. Jalisco. *Pipilo ocai albicollis* occupied brushy understory vegetation.

Fig. 2 Oak woodland on summit of Cerro Viejo, 22 miles south of Guadalupe, 9,000 feet. Jalisco. The hybrids inhabiting this locality were especially abundant in dense undergrowth composed principally of a large woody, red-flowered *Salvia*.





Plate 17. Variation in color and pattern among species of *Aphelocoma* and some groups of *A. coerulescens*. Top to bottom: *A. c. coerulescens*, *A. c. californica*, *A. c. nevadensis*, *A. p. sumichrasti*, *A. ultramarina sordida*, *A. unicolor*. Painting by George Miksch Sutton.

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**SPECIATION AND
ECOLOGIC DISTRIBUTION IN
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GENUS APHELOCOMA**

**BY
FRANK A. PITELKA**

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SPECIATION AND ECOLOGIC DISTRIBUTION IN AMERICAN JAYS OF THE GENUS *APHELOCOMA*

BY

FRANK A. PITELKA

(A Contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

INTEREST in ecological aspects of the species problem has increased in the last decade as a result of the stimulus provided by the recent syntheses of evidence on mechanisms of evolution (Dobzhansky, 1941; Mayr, 1942; Simpson, 1944; and others). This stimulus has come from repeated signs that evolutionary problems should be examined, more than heretofore, in their ecological settings (Jepsen *et al.*, 1949), for it appears that the species problem is even more ecological than genetical.

Studies of the phenomenon of speciation, or the multiplication and diversification of species in space, have helped to bring about this new focus of attention by emphasizing the population basis of evolution and the adaptive significance of "minor" but statistically demonstrable intraspecific differences which align themselves among populations as gradients of change, or clines. In addition, from analyses of ecological and distributional interrelations among closely related species, working principles have been formulated concerning mechanisms which promote ecological segregation or isolation of species. In the present state of our knowledge, these topics are best documented by intensive studies of small taxonomic groups; and in this paper, data are offered on an American group of passerine birds, the jays of the genus *Aphelocoma* (family Corvidae).

Studies of species deal at once with problems of geography, ecology, phylogeny, biometry, and taxonomy, and for this reason the body of facts must be organized about several objectives. In the preparation of this paper, the following were formulated: First, through analyses of structural variation and discontinuities, evidence is provided on the kind and the direction of differentiation which has led to the formation of races and species. The genus *Aphelocoma* differs from the few groups of North American birds intensively studied from this point of view in that it consists of three sympatric species rather than several allopatric species, and its distributional metropolis is not North America proper, but Middle America, where its history is interrelated with that of several other Middle American genera of jays.

Second, the spatial distribution of each race and species has been ascertained as precisely as possible. This evidence provides a partial basis for an understanding not only of race formation in *Aphelocoma* but also of the history of the terrestrial avifauna of Mexico in relation to the northward spread of many of its members into the Neartctic region. Data on habitat distribution are reported so far as available to determine the nature of ecological segregation of the three species of

Aphelocoma and to ascertain the presence or absence of geographic differences in habitat in terms of the vegetation with which each species is associated. These data also bear on the general problem of the effect of different kinds of distributional control among birds.

Third, evidence of the relationships of the members of the genus *Aphelocoma* is offered as a contribution toward the problem of phylogeny of the American jays. Ten genera are recognized at present among the American jays (Hellmayr, 1934); they form a group distinct from other North American corvids having obvious Palearctic affinities (*Corvus*, *Pica*, *Nucifraga*, *Perisoreus*) and are therefore possibly monophyletic (Amadon, 1944a: 6). The American jays are a good example of a group which, although not confined to one or the other hemisphere, has subdivided and apparently undergone considerable evolutionary change since isolation of the ancestral forms in separate continental divisions; the American jays do not include, at present, any species which provides obvious clues to their derivation.

Finally, many nomenclatural and taxonomic problems in the genus *Aphelocoma* are considered—often, of necessity, in the course of discussions of racial characters and interrelationships. Most nomenclatural data are secondary to the objectives of this paper, however, and are segregated in an appendix which includes synonymies, data on types, reviews of nomenclatural history, and lists of specimens examined. Revisions of the nomenclature of *Aphelocoma* have led to a series of changes as a consequence not only of critical review of earlier work but also of the discovery of several new races. Except for Swarth's (1918) review of the Pacific coast races of *A. coerulescens*, there has been no previous comprehensive study of this genus or any segment thereof.

This paper was prepared as a doctoral dissertation which was submitted to the faculty of the University of California in February, 1946. The research on extensive series of specimens was completed the previous autumn. Since then, however, an effort has been made to sample populations not well represented in the original material and to gather additional information on habitat distribution and behavior. Most of the results of this additional research, through 1950, have been incorporated in this report. Certain sections have also undergone some revision since 1946.

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Throughout my investigation, staff members of the Museum of Vertebrate Zoölogy and the Department of Zoölogy, University of California, have extended aid in many ways, and I express my appreciation to them.

MATERIALS

The total number of specimens used was 4,817, approximately 85 per cent of which were assembled at the Museum of Vertebrate Zoölogy. Since jays of the genus *Aphelocoma* are, in general, nonmigratory, no segregation of breeding specimens from less valuable nonbreeding specimens was necessary, and the total represents the quantity of critical material. Collections from which specimens of *Aphelocoma* were examined, together with the names of curators through whom arrangements for study of specimens were made, are as follows:

- Academy of Natural Sciences of Philadelphia (J. Bond) (PAS¹)
- American Museum of Natural History, including the L. C. Sanford collection (J. T. Zimmer and C. E. O'Brien) (AM, LCS)
- British Museum, London (J. D. Macdonald) (BM)
- California Academy of Sciences (R. T. Orr) (CAS)
- Carnegie Museum (W. E. C. Todd and A. C. Twomey) (C)
- Dickey Collections, University of California, Los Angeles (A. J. van Rossem) (DC)
- Museum of Vertebrate Zoölogy, University of California, including the collections of Allan Brooks, R. E. Ellis, Jr., and J. E. Law (MVZ, RE, JEL)
- Chicago Academy of Sciences (H. K. Gloyd) (CS)
- Chicago (formerly Field) Museum of Natural History (K. P. Schmidt, E. B. Blake, and Mrs. E. T. Smith) (CM)
- Colorado Museum of Natural History (A. M. Bailey) (CO)
- Department of Zoölogy, Cornell University (G. M. Sutton)
- Collection of Fish and Wildlife Service (formerly Biological Survey) (J. W. Aldrich) (BS)
- Museum of Comparative Zoölogy, Harvard University (J. L. Peters) (MCZ)
- Los Angeles Museum, including the G. Willett collection (G. Willett) (LAM, GW)
- Museum of Natural History, University of Kansas (E. R. Hall, D. F. Hoffmeister) (KU)
- Museum of Zoölogy, University of Louisiana (G. H. Lowery, Jr.) (LU)
- San Diego Museum of Natural History, including S. G. Jewett collection (L. M. Huey) (SD, SGJ)
- Santa Barbara Museum of Natural History (W. G. Abbott)
- Museum of Natural History, Stanford University (Miss M. Storey and I. L. Wiggins) (SU)

¹ Abbreviations used in citing types and critical specimens in discussion of variation and intergradation.

Museum of Zoölogy, University of Michigan, including the M. M. Peet collection (J. van Tyne, W. H. Burt, and J. J. Hickey) (UM, MMP)
United States National Museum (A. Wetmore and H. Friedmann) (USNM)
Department of Zoölogy, University of Utah (W. H. Behle) (UU)

Additional specimens were examined from the private collections of I. N. Gabrielson, G. M. Sutton, A. G. Prill (AGP), Alex Walker (AW), L. M. Huey (LMH), R. T. Moore (RTM), the late M. S. Ray, and from the departmental collections of the University of British Columbia (through I. McT. Cowan) and the University of California at Davis (through T. I. Storer), Berkeley (through R. M. Eakin), and Los Angeles (through L. H. Miller).

To all the above-named persons and the institutions which they represent, I express my great indebtedness for the kindness and interest shown by them; the scope of my systematic studies has been determined primarily by their coöperative and generous efforts to make available to me the specimens in their care.

Participation in seven field expeditions from the Museum of Vertebrate Zoölogy has enabled me to accumulate data on the distribution, habitat relations, and behavior of the scrub jay, *A. coerulescens*, and the Mexican jay, *A. ultramarina*. *A. c. nevadae* was studied in late May and June, 1940, in the Argus Range and the Grapevine Mountains, in the Horse Spring Range, and on Potosi Mountain along the California-Nevada line east and southeast of Death Valley, and again in April, 1949, in east-central Arizona. To determine relationships of the closely neighboring races *A. c. superciliosa* and *A. c. nevadae*, systematic collecting was conducted on the two sides of the Owens Valley in Inyo and Mono counties, California, in late May and June, 1942. The same problem was studied briefly in June, 1946, and October, 1947, in western Nevada. In June, 1943, *A. c. superciliosa* and *A. c. caurina* were observed in western Tehama and Trinity counties, California, and in October, 1947, the latter race was studied at its northern distributional limits in southwestern Oregon. *A. c. insularis* of Santa Cruz Island, California, was studied in late August and early September, 1948. *A. u. arizonae* was studied in northern Sonora in November, 1946, and in east-central Arizona in April, 1949. (See also footnotes, pp. 309-346.)

Field studies other than expeditions when data on *A. coerulescens* were obtained are as follows. In late May and June, 1941, the geographic relationships of *A. c. oocleptica* and *A. c. caurina* were studied briefly in northern Marin and southern Sonoma counties, California, in the vicinity of Dillon Beach. Records of habitat relations and numbers in a small population of the scrub jay in the Berkeley Hills were obtained during five breeding seasons, 1943-1947; although these data are not reported in this monograph, they afford partial basis for interpretation of certain distributional and systematic problems encountered in the course of my revisionary studies. Field observations on short excursions to various parts of central coastal California, in Sonoma, Napa, Marin, Contra Costa, San Mateo, Santa Cruz, and Monterey counties from 1941 to 1943 and 1946 to 1949 have enabled me to evaluate more precisely data afforded by more intensive local studies and those available in the literature.

My data on the habitat relations of *A. unicolor* are derived entirely from the literature. (But see footnotes, pp. 357-358.)

METHODS OF ANALYZING CHARACTERS

Analyses of variation in the races and species of *Aphelocoma* have been preceded by studies of plumage and of molt which form a necessary preliminary to revisionary studies of the genus. The results of these studies include determination, so far as possible, of interspecific and intraspecific differences in molt. They have been reported in a separate paper (Pitelka, 1945*b*), to which the reader should refer for details.

Extended study of plumages and molt has provided a sound basis for the segregation of first-year birds from adult birds. First-year birds retain remiges, rectrices, and a variable number of greater wing coverts through the postjuvinal molt (*ibid.*: 234, 254). Segregation is based on differences between adult and first-year individuals in form of distal portions of outer rectrices and remiges and in the color of retained versus replaced coverts. It may be added that skull characters commonly used by preparators for aging are not satisfactory in *Aphelocoma*, since a fall-taken bird classified as an adult on the basis of degree of ossification may be a first-year bird.

Segregation of age classes has not been part of any previous study of *Aphelocoma*, nor, in fact, of any other genus of American jays except *Gymnorhinus* (Brodkorb, 1936). Segregation has proved to be of extreme significance in an interpretation of individual and geographic variation; it has enabled me to bring to light certain misconceptions arising from a failure to recognize age classes and to establish on a precise basis intrapopulation and interpopulation differences.

No age or sex difference which I have studied is absolute, but in almost all characters there are statistical differences which, considered singly, are often not significant from a purely statistical point of view, but which are significant from a biological point of view, for two reasons. First, in comparisons of dimensions of sex and age groups within a given sample, although magnitude of difference varies from one character to another, most of the averages are successively smaller for first-year males and adult and first-year females. One important exception is that of wing and tail dimensions in *A. ultramarina* and *A. unicolor*, in which these dimensions average smaller in first-year males than in adult females. The same exception serves to emphasize the necessity for segregation of age classes.

A second reason for regarding mensural differences as biologically significant when, singly, they are statistically insignificant, is the fact that a given difference often represents part of a trend which is evident in a geographic series of populations and which, further, is demonstrable independently in both sex groups or in all four sex and age groups. Refined statistical methods adapted to test the particular type of data accumulated here in order to reveal significance where ordinary tests fail to do so have not been used; but the observed consistencies are of such a high positive order that there is little doubt in my mind that the interpretations of variation based on them are valid. Details of individual and sex variation are presented in descriptive sections that follow.

Tests of significance used in comparisons of mensural characters in different populations are the graphic method of Dice and Leraas (1936), in which the criterion of significance is overlap between bars representing twice the standard

TABLE 1

TONES, HUES, AND INTENSITIES OF BLUE OCCURRING ON DORSUM, REMIGES, AND RECTRICES IN GENUS *APHELOCOMA*¹

Class	(Hues)				brighter I ²
	purplish ←			→ bluish	
	A	B	C	D	
I	a Asurite Blue	Cyanine Blue	Prussian Blue		
II	a Indulin Blue	Dusky Blue	Hortense Blue	darker ↑	
	b Deep Dull Viola- ceous Blue	Eton Blue	Gendarme Blue	(tones)	II ³
	d Grayish Viola- ceous Blue	Chapman's Blue	Jay Blue	↓ lighter	
			Vanderpoel's Blue		
III	a Nigrosin Blue	Indigo Blue Dark Tyrian Blue Tyrian Blue Light Tyrian Blue	Deep Orient Blue Orient Blue Alice Blue	darker ↑ (tones) ↓ lighter	III
IV	a			darker ↑ (tones)	IV
	b Slate Blue			↓ lighter	
	c Deep Dutch Blue				
	d				duller

¹ Only those of Ridgway's colors used in textual descriptions are tabulated here.² Class I consists of the darkest shades of pure colors; class II, III, and IV consist of shades, full colors, or tints of "broken" colors (see text, p. 201, also Ridgway, 1912-3, 16-10).³ This series of three colors is intermediate between A and B.

errors of two means, and the formula d/σ_d (difference in means divided by the standard error of the difference; Simpson and Roe, 1939: 192-195), a difference (d) between two means being significant when the derived value is greater than 3. (See also Hubbs and Perlmutter, 1942.)

Evaluation of color characters has of necessity been qualitative. Descriptions are based on specimens in fresh plumage obtained during or after the fall molt; most of the specimens were collected in September, October, or November. Study of color characters was confined to periods of clear weather; sunlight was avoided by using a large west-facing window during mornings or, less frequently, a large north-facing window during afternoons. Comparative color evaluations in periods of clear, hazy, and cloudy weather served to emphasize strongly the importance of adhering to this procedure. Differences in color evaluations due to different light conditions were, as might be expected, especially significant in the various grades of blue.

Color terms of Ridgway (1912) are used. Because the number of terms for different gradations of blue is large and because not all readers may have access to Ridgway's work, it seems worth while to tabulate the terms in a manner which will seriate them according to the three basic color scales. Also, Ridgway's terms for different gradations of blue are not so descriptive as are those for browns and grays. Table 1 can thus serve as a ready reference when questions on comparative coloration arise in the study of any one race. Interracial differences in blue coloration are most strongly displayed by the color of the pileum; those in blue color of the sides of head and neck, wings, and tail, and when any blue color is present, pectoral collar and under tail coverts, correspond in direction to those of the pileum, but of course different hues, tones, or intensities are involved. Refer to table 2 for grades of blue occurring on under tail coverts of *A. coerulescens*.

An observed color is, of course, more frequently intermediate between any two standard colors of Ridgway than it is referable to one of them. This fact has led to the adoption of a system of designating colors in Ridgway's terms which must be understood if the following descriptions are to be interpreted correctly. Taking as an example the most complex series of colors, the different grades of blue, Ridgway's terms have been arranged in table 1 to show gradation from pure blue to purplish blue (right to left, classes indicated by capital letters), from dark to light (top to bottom between horizontal lines, classes indicated by small letters), and from bright to dull or less gray to more gray (top to bottom, four classes indicated by roman numerals). The bases of these three gradations are, respectively, change in hue, tone, and intensity. Each series represents one of the three basic color scales. Ridgway (1912:18) declined to provide a term for the third, that is, graded change due to increasing increments of neutral gray, which, added to pure colors, produce "broken" colors (*ibid.*: 8, 16-19). The term "intensity" is arbitrarily adopted for the third scale.

In the scheme of hues and shades within any one intensity class, as shown in table 1, a natural color may fall between neighboring shades of one hue or between neighboring hues of one shade in vertical, horizontal, or diagonal directions. Further, a natural color may be intermediate in one of these directions and also may fall between neighboring intensities. Departure of any observed color from

the arbitrary colors of Ridgway is indicated in textual descriptions by such usage as "Chapman's Blue—Tyrian Blue," or "Deep Orient Blue—Dark Tyrian Blue," the observed color being intermediate between or closer to the first of the two arbitrary grades.

The following linear measurements were taken from skins. (1) Wing, the chord (Baldwin, Oberholser, and Worley, 1931:76). (2) Tail, from space between rectrices 1-1 at their base to the tip of the longest rectrices (1-1 or 2-2). (3) Length of bill, from anterior rim of nostril to tip. (4) Depth of bill, from culmen to lower edge of ramus at anterior margin of nostril (actually the chord of the lateral surface of the bill; *ibid.*:19). (5) Width of bill, from one tomium to the other at the

TABLE 2
GRADES OF BLUE OCCURRING ON UNDER TAIL COVERTS OF APHELOCOMA COERULESCENS¹

Class	A	B	C	
I	a Clear Windsor Blue b Light Windsor Blue c Pale Windsor Blue	Light Tyrian Blue Columbia Blue Light Columbia Blue	Orient Blue Alice Blue	I
II	a Slate Blue b Deep Dutch Blue c Dutch Blue	Delft Blue Parula Blue Cadet Gray		II
III	a b c	Clear Payne's Gray Light Payne's Gray Pale Payne's Gray	Deep Green-Blue Gray Clear Green-Blue Gray Pale Green-Blue Gray	III

¹ See text, p. 201, and table 1 for explanation of color categories.

anterior margin of the nostrils. This measurement is not described by Baldwin *et al.* (*ibid.*:21), but they emphasize the desirability of taking depth and width measurements in the same transverse plane of the bill. (6) Tarsus, from joint between tibiotarsus and tarsometatarsus behind to the middle of the distalmost undivided scute on the front which is aligned with metatarsal scutes (actually a diagonal of the tarsus; *ibid.*:107). The critical scute at the distal end of the metatarsus is not bent or curved to fit over the scutes which more or less cover the bases of the phalanges and which may not be complete; also, it is that scute the distal margin of which is usually on a line projected anteriorly from the lateral ridge of the hind toe. (7) Hind toe without claw, from palmar fold on ventral side to tip beneath claw. The palmar fold is in line with the posterior margin of the metatarsus at its distal joint; if, as is true occasionally, a palmar fold is not evident, then a line projected from the posterior tarsal margin to the palmar surface serves as the proximal extreme of this measurement. (8) Middle toe without claw, from proximal edge of the proximalmost movable scute at the junction of middle and inner toes to the claw on the upper side.

All available records of weights have been classified according to population limits adopted for statistical treatment of measurements. Averages and extremes are given for males and females. No significant difference was found between age

groups of each sex. No data are available to determine presence or absence of significant seasonal variation; since the species of *Aphelocoma* are nonmigratory, it seems probable that no such variation occurs, except possibly in the northern and interior races of the scrub jay, *A. c. woodhousei* and *nevadae*. Available evidence suggests that nonmigratory species do not undergo significant seasonal change in weight as do migratory species (Wolfson, 1945:117; see also review of Farner, 1950:111-112).

TABLE 3

NUMBERS AND DISTRIBUTION OF SPECIES IN TEN AMERICAN GENERA OF JAYS AS PRESENTED BY HELLMAYR (1934)

Genera	North America	Middle America	South America
<i>Gymnorhinus</i>	1		
<i>Cyanocitta</i>	1 ¹ ---	--- 1	
	1		
<i>Aphelocoma</i>	1 ¹ ---	--- 1	
		2	
<i>Calocitta</i>		1	
<i>Psilorhinus</i>		2	
<i>Cissilopha</i>		4	
<i>Cyanolyca</i>		1 ---	--- 1 ^{1, 2}
		4	2 ²
<i>Xanthoura</i> ⁴		1 ---	--- 1 ¹
<i>Cyanocorax</i>		1 ---	--- 1 ¹
		1	8
<i>Uroleuca</i> ⁴			1
Totals.....	4	19	14

¹ Present also in Middle America.

² Although combined under one name by Hellmayr (1934:46) and here so indicated, *pulchra* of South America and *oculata* of Central America are doubtfully conspecific.

³ One of these, *furcosa*, is almost certainly a race of the other, *viridis-cyana*.

⁴ Doubtfully distinct from *Cyanocorax*; see Amadon, 1944a:8.

SURVEY OF THE GENUS APHELOCOMA

It is not possible to characterize the genus *Aphelocoma* in any but superficial terms, since no studies of comparative morphology of garruline genera have been made, with the exception of Ashley's (1941) work on the humerus of North American corvids. According to Ridgway (1904:323), members of the genus *Aphelocoma* are "medium-sized or rather small jays, without any crest, and with the prevailing color uniform blue or blue and gray." Absence of conspicuous black bands on wings and tail (Baird, 1858:584) distinguishes *Aphelocoma* from *Cyanocitta* but not from other closely related genera as *Cyanolyca*. Other structural features mentioned in characterizations of *Aphelocoma*, such as form of nostril, extent of nasal feathering, and wing-tail proportions (Baird, *ibid.*), are not diagnostic and, in fact, are similar to those of other genera.

Ridgway (1904:324) noted close relationships of *Aphelocoma* with *Cyanolyca*, two Central American species of which are structurally similar to *Aphelocoma* and differ only in style of coloration, and with *Cyanocitta*, from which *Aphelocoma*

differs in the absence of any crest. In a recent review of the genera of corvids, Amadon (1944a:6) has proposed that close relationship of *Aphelocoma*, *Cyanocitta*, *Cyanolyca*, and another Central American genus, *Cissilopha*, be expressed nomenclaturally by placement of all species of these genera, totaling sixteen, in

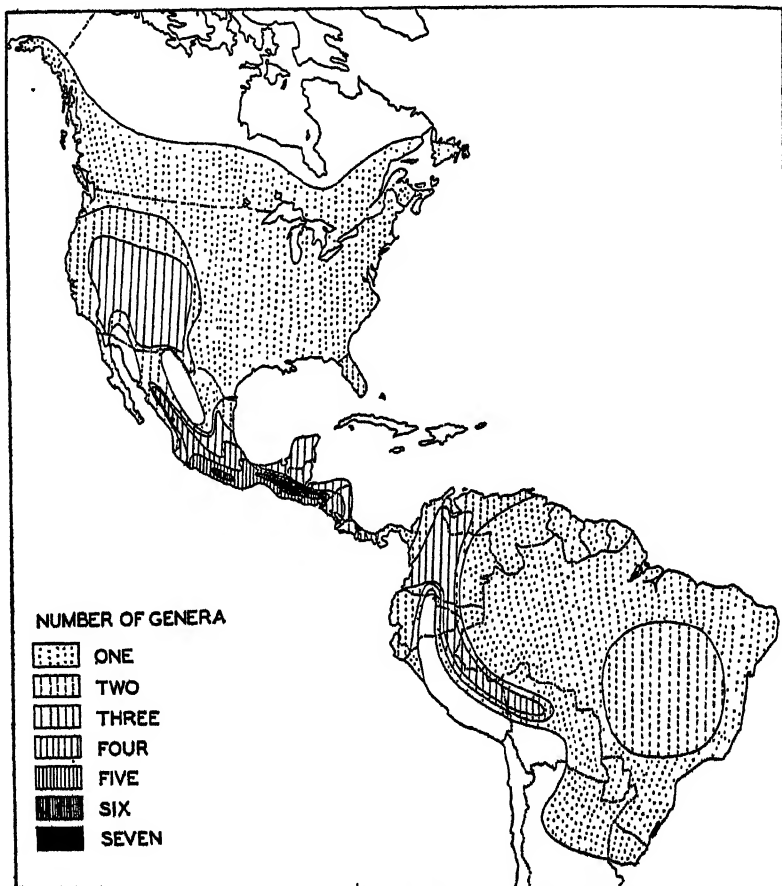


Fig. 1. Geographic density of ten genera of American jays. This group includes all genera of American Corvidae except *Corvus*, *Nucifraga*, *Pica*, and *Perisoreus*. See table 3.

one genus, *Cyanocitta*. He is correct in pointing out (*ibid.*:7) that the four genera as defined by Ridgway (1904) are "characterized by extremely variable and intergrading characters." But much-needed data on comparative morphology, behavior, and ecology to determine satisfactorily generic limits are not available. Ashley's (1941) study of the humerus reveals similarities of *Aphelocoma* to *Cyanocitta* and thus provides partial morphological evidence supporting Amadon's proposal. Ashley, however, did not have material of any of the Central American genera, among which, I believe, the best clues to relationships will be found.

Aphelocoma is one of ten garruline genera confined to the Western Hemisphere

and concentrated in Central America. To show their geographic density in the main divisions of the Western Hemisphere, table 3 and figure 1 have been prepared. Table 3 includes the monotypic genus *Gymnorhinus*, which, on the basis of preliminary studies of comparative osteology, is here tentatively regarded as part of the complex of American jays (see also Ashley, 1941:194; Amadon, 1944a:7). The map, based largely on data and nomenclature of Hellmayr (1934), is generalized and diagrammatic, but serves to illustrate several important points.

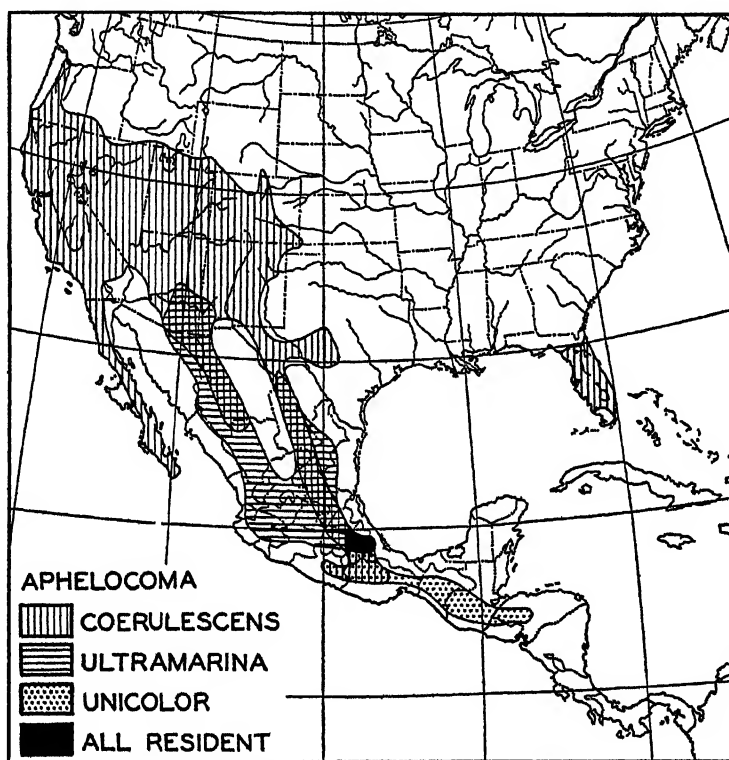


Fig. 2. Generalized distribution of jays of genus *Aphelocoma*. For discontinuities in range of each species see detailed maps; also see legend of figure 10.

From this map it is evident that as many as seven genera may occur in extreme southeastern Mexico and Guatemala; of the Middle American genera listed in table 3, only *Cyanocorax* is absent from these areas. A subsidiary concentration occurs in the Mexican state of Guerrero, where *Psilorhinus* and *Cyanocorax* do not occur. Griscom (1932) has recorded seven genera from Guatemala; however, the extent to which these approach or overlap locally, from the standpoints of both geographic and ecologic segregation, needs to be determined in detail.

The map also shows that approximately the same number of genera have been involved in dispersal to the north and south, although no one genus is involved in both directions (table 3). Most of the Isthmus of Panama is inhabited by but one genus (and one species, *Cyanocorax affinis*). There are thus discontinuities in the

ranges of two of the genera; these are *Xanthoura*, which is monotypic (but see table 3), and *Cyanolyca*. Among these ten genera, *Aphelocoma* is one distributed over part of North America as well as most of Central America.

Some indication of the extent of geographic radiation among American jays is provided by the distribution of the thirty-two presently recognized species among the ten genera (table 3). Nineteen occur in Middle America, two extending into North America and three others into South America. Two species are confined to North America, and eleven, mostly members of the genus *Cyanocorax*, are confined to South America. It should be noted that corvids of supposedly recent derivation from the Palearctic region are absent from South America; these include the genera *Corvus*, *Neofriga*, *Pica*, and *Perisoreus*, in which are included eight species exclusive of insular forms.

It should be borne in mind that this review of the general features of geography and dispersal of the American jays is based on Ridgway (1904) and Hellmayr (1934), where the evidence is largely preliminary in character. Although further research is not expected to alter the gross aspects of the known distributional picture, the interpretation and biological significance of that picture can come only through intensive studies of each genus.

Of the total of thirty-two species, three are members of the genus *Aphelocoma*. Their distributional ranges overlap in southeastern Mexico (fig. 2). Two, *A. ultramarina* and *A. unicolor*, are Middle American, although the former extends northward into Arizona and Texas; the third and most widely distributed, *A. coerulescens*, occurs from southern Mexico northward over southwestern North America and in Florida. The following synoptic outline provides an introduction to the forms included in the genus *Aphelocoma* and to their interrelationships.

Under parts light gray or white and contrasting in color with dark upper parts.

Pectoral collar usually present, often well developed; superciliary line present; throat streaked, differing in color from lower breast; color contrast between back and pileum strong; tail longer than wings.

coerulescens rassenkreis

"californica" group of races

Aphelocoma coerulescens californica, central coast of California

Aphelocoma coerulescens ocleptica, San Francisco Bay region

Aphelocoma coerulescens aurina, northern coast of California

Aphelocoma coerulescens obscura, coast of southern California and northern Baja California

Aphelocoma coerulescens cana, Eagle Mountain, interior Riverside County, California, and (?) interior northern Baja California

Aphelocoma coerulescens oactophila, central Baja California

Aphelocoma coerulescens hypoleuca, Cape region, Baja California

Aphelocoma coerulescens superciliosa, interior California and south-central Oregon

Aphelocoma coerulescens immanis, north-central Oregon

Aphelocoma coerulescens insularis, Santa Cruz Island

"woodhousei" group of races

Aphelocoma coerulescens woodhousei, southern Rocky Mountains, New Mexico, and western Texas

Aphelocoma coerulescens nevadae, Great Basin and Arizona

Aphelocoma coerulescens grisea, Sierra Madre Occidental of Durango and Chihuahua

Aphelocoma coerulescens texana, west-central Texas

Aphelocoma coerulescens cyanotis, east-central Mexico

"*sumichrasti*" group of races

Aphelocoma coerulescens sumichrasti, Veracruz, Puebla, and Oaxaca

Aphelocoma coerulescens remota, Guerrero

Aphelocoma coerulescens coerulescens, Florida

Pectoral collar broad and obsolescent or absent; superciliary line absent; throat and lower breast similar in color; color contrast between back and pileum weak; tail shorter than wings.

ultramarina rassenkreis

"*wollweberi*" group of races

Aphelocoma ultramarina arizonae, Arizona, southwestern New Mexico, and northwestern Mexico

Aphelocoma ultramarina wollweberi, Sierra Madre Occidental, chiefly Durango

Aphelocoma ultramarina gracilis, north-central Jalisco, and Nayarit

"*sordida*" group of races

Aphelocoma ultramarina ouachui, northeastern Mexico and southwestern Texas

Aphelocoma ultramarina sordida, east-central Mexico

"*ultramarina*" group of races

Aphelocoma ultramarina ultramarina, Veracruz, Puebla, Michoacán, etc.

Aphelocoma ultramarina colmae, southern and western Jalisco and Colima

Aphelocoma ultramarina ssp.?, central Jalisco, southeastern Nayarit

Under parts blue or purplish blue and similar in color to upper parts.

unicolor rassenkreis

Aphelocoma unicolor unicolor, Guatemala and Chiapas

Aphelocoma unicolor oaxacae, Oaxaca

Aphelocoma unicolor concolor, Veracruz, Puebla, and México

Aphelocoma unicolor guerreroensis, Guerrero

Aphelocoma unicolor griscomi, El Salvador and Honduras

VARIATION AND INTERRELATIONSHIPS AMONG RACES OF APHELOCOMA COERULESCENS

The scrub jay, *A. coerulescens*, consists of eighteen presently recognized geographic races, which, in the light of differentiating characteristics and degree of distinctness displayed by each, can be divided into four groups. The first of these, the "*californica*" group, consists of ten races distributed in Oregon, California, and Baja California southward to the Cape. The races are *californica*, *oocleptica*, *caurina*, *obscura*, *cana*, *cactophila*, *hypoleuca*, *superciliosa*, *immanis*, and *insularis*. The second, or "*woodhouseii*," group consists of five races distributed in the Great Basin and Rocky Mountains and south into Mexico east and west of the central plateau. The races are *woodhouseii*, *nevadae*, *texana*, *grisea*, and *cyanotis*. The third, or "*sumichrasti*," group consists of two races, *sumichrasti* and *remota*; it occurs in southeastern Mexico and along the Sierra Madre del Sur. The fourth group is represented by but one race, *coerulescens* of Florida.

The accounts of the races which follow are presented in the order given above. It is necessary beforehand, however, to characterize and compare the four divisions of the *coerulescens* rassenkreis. For this purpose the races *californica*, *woodhouseii*, and *sumichrasti* will serve as representatives of their respective groups.

The "*californica*" group is characterized by a contrasting plumage pattern. The degree of contrast exceeds that of the remaining forms of the *coerulescens* rassenkreis. Under parts are light-colored or white. Under tail coverts are blue, tinged with blue to varying degree, or white. The collar pattern is well developed. Blue

areas are dark and more or less purplish. The back is brown and contrasts with the color of the head and hind neck.

The "*woodhouseii*" group, on the other hand, lacks the contrast of the plumage of *californica*. Under parts are gray. Under tail coverts are blue. Blue areas are less purplish and more grayish. The collar pattern is less contrasting because of the obscuring effect of the otherwise gray under parts, but actually the feathers of the mid-region of the collar are edged with more blue than in *californica*. The back is gray brown and there is only slight contrast between the hind neck and back.

The "*sumichrasti*" group displays a somewhat more contrasting plumage than *woodhouseii*, but not to the degree of *californica*. This difference is due to an intensification of color of the upper parts and a lightening of the under parts through absence of gray. Thus, blue areas are brighter than in *woodhouseii*, but not purplish as in *californica*. Under tail coverts are white. The collar pattern is reduced, there being little or no blue except laterally near the bend of the folded wing. Under parts are light-colored or white. The back is brown and more or less similar to that of *californica*. Unlike more northern groups, the superciliary line is poorly developed.

Coerulescens has a plumage almost as contrasting as that of *californica*. Blue areas are slightly duller and grayer than in *woodhouseii*, approximately of the same hue and tone as, but slightly grayer than, in *sumichrasti*, and not so purplish, dark, and bright as in *californica*. The collar pattern is well developed, more so than in *californica* or *woodhouseii* in that the mid-region bears considerably more blue than either. The collar band is thus more or less conspicuous in spite of the fact that the under parts are grayish as in *woodhouseii*. The under tail coverts are always blue. The back is grayish brown, but lighter than in *woodhouseii*, and thus contrasts with the color of the head and hind neck. Only this Floridan form displays any peculiar color characters. These are, first, a white forehead, the white extending laterally and posteriorly as a more or less broad band over the superciliary region and, second, obscure streaking of the back and of the breast below the collar.

In size, members of the "*californica*" group are characterized by a heavy bill and short wings. This group includes the largest (*insularis*) and one (*cactophila*) of the two smallest races of the scrub jay; the other of approximately the same size is *coerulescens* of Florida. In the "*woodhouseii*" group the bill is longer (see p. 209), but not so heavy basally; the wings are relatively longer. In the "*sumichrasti*" group the bill is heavier than in *californica* but only slightly longer, and not so long as in *woodhouseii*; the wings are appreciably longer than in remaining races of the scrub jay. In *coerulescens* the bill is shorter and strikingly broader and the wings are shorter than in remaining races. Quantitative measures of these comparisons are the differences between adult males of *californica* and of representative races of the other groups in terms of percentage of values for *californica*.

The groupings of races of *A. coerulescens* are unsatisfactory in that they involve an arbitrary separation of interior northern American and Mexican races into two groups, "*woodhouseii*" and "*sumichrasti*," which are bridged by three races more or less intermediate between them, *texana*, *cyanotis*, and *grisea*. Depending on the particular character under study, these races may be closer to either one or the other of the two groups. However, the separation adopted here seems to me

the most nearly satisfactory from the geographic as well as the structural standpoint. At any rate, the northernmost and southernmost races represent striking extremes in racial differences and merit recognition as groups on a level with the Floridan race, on the one hand, and Pacific coast races, on the other. Moreover, it appears that the present contact between the "*woodhouseii*" and "*sumichrasti*" groups is a secondary one.

	<i>californica</i> (table 4)	<i>woodhouseii</i> (table 28)	<i>sumichrasti</i> (table 36)	<i>coerulescens</i> (table 38)
	mm.	per cent	per cent	per cent
Wing.....	123.00	+ 6.4	+17.0	- 6.6
Tail.....	137.30	+ 4.8	+ 6.7	+ 3.8
Bill length.....	18.82	+ 5.9	+ 1.5	- 4.3
Bill depth.....	9.16	- 6.4	+ 5.3	+ 0.7
Bill width.....	8.75	- 7.2	+ 2.9	+ 8.5
Tarsus.....	40.62	- 2.2	+ 3.3	- 8.3
Hind toe.....	13.38	- 7.5	+ 0.4	- 7.5
Middle toe.....	19.90	- 6.2	+ 1.3	- 5.5

THE "CALIFORNICA" GROUP OF RACES

Aphelocoma coerulescens californica

Description and racial characters. Male: adult fall plumage.—Upper parts: pileum, hind neck, and sides of neck Deep Dull Violaceous Blue (tending slightly toward Deep Cadet Blue); auricular region brownish black, rarely black, terminal portions of feathers with violaceous blue; sub-auricular and suborbital regions violaceous blue, but darker; lores black, faintly and variably spotted with dull white; white, somewhat irregular superciliary line, narrow anteriorly; back dull grayish brown (Hair Brown) suffused slightly with bluish gray; scapulars and rump more bluish gray (tending toward Tyrian Blue); upper tail coverts brighter (Chapman's Blue—Tyrian Blue).

Under parts: chin, throat, and mid-chest white, seemingly streaked finely with gray and black, an effect due to absence of barbs from terminal portions of rachises, which become black on chin, together with variable graying of lateral margins of vanes; sides of throat and chest dull violaceous blue, extending toward middle of upper breast but not enclosing anterior white area; median feathers along posterior margin of white area appear streaked, but actually edged laterally with grayish blue, those to the sides with dull violaceous blue; lower breast pale drab gray (Pale Smoke Gray to Smoke Gray), becoming slightly darker on sides and lighter (Pale Smoke Gray to dull white) toward crissum; ankle feathers Light Mouse Gray to Mouse Gray, rarely touched with pale blue; under tail coverts tinged variably with pale blue (approaching Pale Payne's Gray to Russian Blue), the longest feathers usually tinged most strongly; under tail coverts tinged in approximately 75 per cent of specimens, otherwise white.

Wings and tail: remiges and feathers of alula dull dark blue (Tyrian Blue to Dark Tyrian Blue); primaries dull dark brown (Fuscous) distally; inner webs of all remiges except innermost secondaries similar in color; fifth primary longest; innermost secondaries and coverts (especially marginal coverts) slightly brighter (Chapman's Blue—Tyrian Blue); under wing coverts dull gray (Mouse Gray), tipped with blue near wing margin; rectrices similar to remiges in color (Tyrian Blue—Dark Tyrian Blue). Wing-tail ratio, 0.896:1. (See table 4 for other statistical data.)

Bill: black, heavy; hook short and practically straight; culmen more or less sharply curved terminally.

Feet: black.

Iris: brown.

TABLE 4

MEASUREMENTS OF *A. C. CALIFORNICA* FROM CENTRAL COASTAL CALIFORNIA
(Santa Cruz County to Central San Luis Obispo County)

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	22	119.0-128.0	123.00±0.51	2.40	1.95
		First-year..	25	115.0-125.2	120.08±0.53	2.67	2.22
	F	Adult.....	25	113.8-124.7	119.00±0.57	2.87	2.41
		First-year..	21	112.9-121.0	115.90±0.55	2.52	2.18
Tail	M	Adult.....	20	132.3-143.2	137.30±0.79	3.53	2.57
		First-year..	26	124.8-139.4	131.62±0.66	3.36	2.55
	F	Adult.....	25	124.7-140.3	132.12±0.85	4.26	3.25
		First-year..	18	122.3-131.8	126.00±0.60	2.56	2.03
Bill length	M	Adult.....	22	17.4- 20.9	18.82±0.18	0.87	4.62
		First-year..	24	16.7- 20.7	18.98±0.21	1.02	5.37
	F	Adult.....	24	16.8- 20.2	18.45±0.18	0.88	4.76
		First-year..	15	16.7- 18.9	17.68		
Bill depth	M	Adult.....	19	8.7- 9.8	9.16±0.07	0.31	3.38
		First-year..	21	8.2- 9.5	9.10±0.09	0.42	4.61
	F	Adult.....	25	8.3- 9.5	8.89±0.07	0.33	3.71
		First-year..	15	8.0- 9.3	8.56		
Bill width	M	Adult.....	22	7.9- 9.4	8.75±0.09	0.43	4.92
		First-year..	24	7.3- 9.7	8.65±0.12	0.61	7.00
	F	Adult.....	25	7.6- 9.5	8.45±0.09	0.43	4.99
		First-year..	15	7.2- 9.3	8.21		
Tarsus	M	Adult.....	22	38.3- 43.2	40.62±0.28	1.32	3.25
		First-year..	28	38.0- 42.2	40.18±0.19	1.00	2.49
	F	Adult.....	24	38.0- 41.5	39.73±0.17	0.86	2.16
		First-year..	20	36.6- 40.7	38.89±0.21	0.93	2.39
Hind toe	M	Adult.....	22	12.3- 14.5	13.38±0.11	0.50	3.74
		First-year..	28	12.2- 14.0	13.24±0.08	0.45	3.39
	F	Adult.....	25	11.8- 13.8	12.90±0.10	0.52	4.03
		First-year..	22	12.0- 13.8	12.73±0.10	0.46	3.61
Middle toe	M	Adult.....	22	18.8- 21.7	19.90±0.13	0.61	3.06
		First-year..	28	18.3- 20.6	19.61±0.11	0.61	3.12
	F	Adult.....	25	18.1- 20.3	19.20±0.12	0.62	3.28
		First-year..	21	17.5- 20.3	19.04±0.15	0.68	3.57
Weights (gm.)	M	14	88 -106	94.9		
	F	9	80 - 93	85.9		

Female: adult fall plumage.—Similar to male, except for generally paler (grayer, less bluish) coloration and reduced markings on mid-chest; blue on sides of chest generally less extensive, reduced and replaced partially by grayish brown; pileum, hind neck, and sides of chest of slightly duller, less purplish blue; suborbital and subauricular regions often less bluish, more brownish black; under tail coverts less frequently tinged with blue (in approximately 50 per cent of specimens). Consistently smaller in all measurements (see tables 4 and 5, fig. 3); differences range from 2 per cent in bill length to 3.8 per cent in tail length.

TABLE 5

AVERAGE MEASUREMENTS OF SEX AND AGE GROUPS OF APHELOCOMA COERULESCENS EXPRESSED AS PERCENTAGE OF MEASUREMENTS OF ADULT MALES

	First-year males	Adult females	First-year females
A. C. CALIFORNICA (table 4)			
Wing.....	97.6	96.7	94.2
Tail.....	95.9	96.2	91.8
Bill length.....	100.8	98.0	93.9
Bill depth.....	99.3	97.1	93.4
Bill width.....	98.8	96.6	93.8
Tarsus.....	98.9	97.8	95.7
Hind toe.....	98.9	96.4	95.1
Middle toe.....	98.5	96.5	95.7
A. C. OCCIDENTICA (table 8)			
Wing.....	97.9	96.8	94.3
Tail.....	95.2	94.7	92.1
Bill length.....	98.5	95.5	92.7
Bill depth.....	97.8	94.7	92.7
Bill width.....	98.6	94.6	92.7
Tarsus.....	99.1	97.6	95.9
Hind toe.....	99.1	97.3	95.6
Middle toe.....	99.2	96.5	96.2

Male and female: first-year fall plumage.—Similar to adult except that remiges and rectrices of juvenal plumage are retained through postjuvenal molt, as are greater primary coverts, greater secondary coverts in variable number, and feathers of alula; pileum, hind neck, and sides of head and chest average less purplish than adults of corresponding sex; collar markings reduced in females, replaced by gray; color of back and remaining under parts comparable to adults. Smaller than adults of corresponding sex; first-year males approximately intermediate between adult males and adult females. (See tables 4 and 5, fig. 3.)

Male and female: juvenal plumage.—Upper parts: pileum, hind neck, suborbital and auricular regions, sides of upper chest, and upper tail coverts dark dull grayish brown (Fuscous, occasionally tending toward Hair Brown); pileum tinged usually and in varying degree with dull blue; back, scapulars, and wing coverts (but not greater coverts) lighter (Hair Brown); superciliary line narrow, irregular, dull brownish white, broadening into streaked supra-auricular patch.

• Under parts: chin, throat, and middle of chest dull white (approaching Pale Smoke Gray); sides of throat and chest dull brown (Hair Brown to Chaetura Drab), extending toward middle of breast; lower breast and sides of belly dull white, variously tinged with pale brownish gray; under tail coverts and ankle feathers dull brownish gray; belly dull white.

Wings and tail: remiges duller than in adults (Delft Blue—Deep Delft Blue); distal portions of primaries and inner webs of all except innermost remiges dull dark brown, slightly lighter

than in adults; middle and marginal coverts dull brown (Hair Brown), middle coverts tinged distally with dull blue; greater coverts and feathers of alula similar to remiges, but tipped with dull brown; rectrices similar to remiges in color.

Bill and feet: varying shades of brown and brownish black, depending on age.

Individual, sex, and age variation.—Among fresh-plumaged adult males taken along the coast of central California, there is slight variation in violaceous blue of the head. Of two specimens which represent extremes in the series, one is more

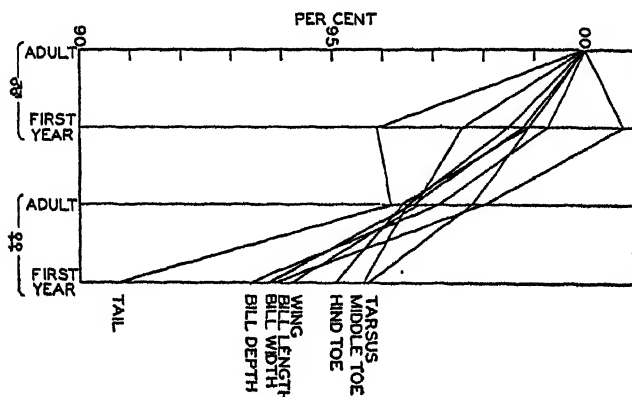


Fig. 3. Comparison of average measurements of sex and age groups of *Aphelocoma coerulescens californica* (table 4); averages of first-year males, adult females, and first-year females expressed as percentage of those of adult males.

purplish and generally darker (MVZ 72597); the other is comparable to typical *californica* except in shade of blue, which is Chapman's Blue—Deep Dull Violaceous Blue (CM 142456). The blue of wings and tail varies correspondingly with head coloration, but variation is less evident and the shade of blue is always duller. Under tail coverts are tinged with pale blue or gray in approximately 75 per cent of males, 50 per cent of females; otherwise they are white. Color of back and under parts does not vary appreciably. In females, coloration of head, wings, and tail varies from the average of males to a duller extreme somewhat beyond that of males; thus there is considerable overlap in the color range, but in comparing series of the two sexes the less purplish coloration of females is clearly evident. Back coloration is similar to that of males. Chest markings are present to a variable extent in both sexes; in females they are typically reduced and replaced partially by grayish brown.

Among first-year birds the pileum, hind neck, and sides of neck and chest average slightly duller and less purplish than adults of corresponding sexes. First-year males are more variable than adult males. Individual variants may be as richly colored as adults; the difference in average shade of blue is due to the fact that more individuals tend toward Chapman's Blue. First-year males average more purplish than adult females, however. First-year females, comparably duller and more variable than adults, reach Tyrian Blue—Chapman's Blue in certain individuals (CM 51599). Whereas the collar pattern of first-year males is generally

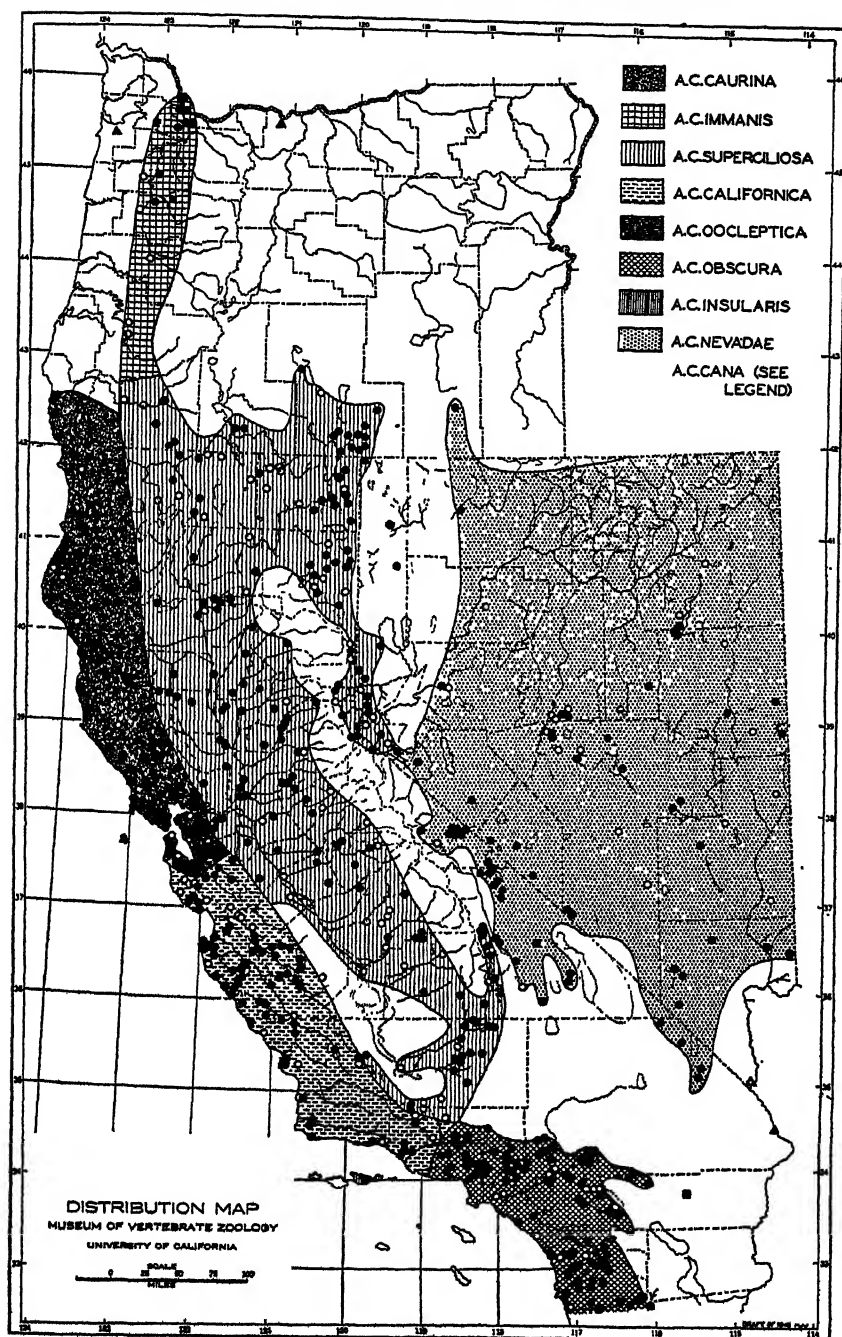


Fig. 4. Distribution of races of *Aphelocoma coerulescens* in Oregon, California, and Nevada. Dots indicate localities from which specimens have been examined; circles, localities reported in literature; squares, type localities; triangles, vagrants. Distribution of *A. c. cana* is shown by square in central Riverside County and dot with arrow at

similar to that of adult males, in first-year females collar markings are reduced even more than in adult females, so that feathers of the middle of the chest may show little or no gray edgings. Back coloration of first-year birds is comparable to that of adults.

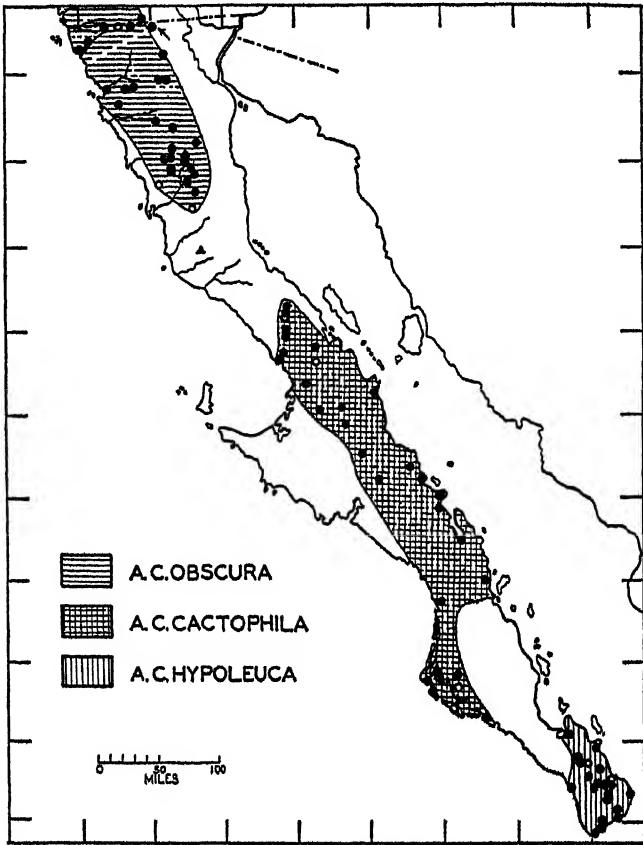


Fig. 5. Distribution of races of *Aphelocoma coerulescens* in Baja California. Dots indicate localities represented by specimens; circles, localities reported in the literature; squares, type localities; triangles, vagrants. Distribution of *A. c. oana* is indicated by dot with arrow near California border.

Size differences between sex and age groups are given in table 5 as percentage of measurements of adult males. In addition to data for *A. c. californica*, those for *A. c. oocleptica* of the eastern San Francisco Bay region are included for comparative purposes. Differences in wing length, which amount to almost minus 6 per cent in first-year females, agree closely in the two races. This is true also of measurements of feet both interracially and intraracially. Slight discrepancies between the two races in differences evident in bill and tail dimensions may be due to sampling error. But the evidence of the magnitude of intraspecific differences between age and sex groups is clearly shown.

TABLE 6

MEASUREMENTS OF A. C. CALIFORNICA FROM INNER COAST RANGES AND ADJOINING LOWLANDS OF
CENTRAL CALIFORNIA
(Eastern and Central Santa Clara County South to Northern San Luis Obispo County)

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	16	118.7-129.7	124.87±0.80	3.20	2.56
		First-year..	34	118.5-129.6	123.06±0.43	2.50	2.03
	F	Adult.....	6	115.8-123.1	119.17		
		First-year..	12	110.6-122.7	116.42		
Tail	M	Adult.....	15	130.6-147.1	138.87		
		First-year..	34	125.6-140.5	134.21±0.63	3.68	2.74
	F	Adult.....	6	124.3-140.8	133.83		
		First-year..	10	120.6-135.9	126.50		
Bill length	M	Adult.....	16	17.6- 20.9	19.11±0.21	0.83	4.34
		First-year..	16	17.8- 20.3	19.23±0.18	0.73	3.79
	F	Adult.....	6	16.5- 18.7	17.65		
		First-year..	10	16.7- 18.8	17.77		
Bill depth	M	Adult.....	16	8.5- 9.9	9.24±0.09	0.38	4.11
		First-year..	16	8.5- 9.9	9.19±0.10	0.42	4.57
	F	Adult.....	6	8.2- 9.1	8.75		
		First-year..	10	8.1- 9.1	8.59		
Bill width	M	Adult.....	16	8.0- 9.0	8.56±0.07	0.27	3.15
		First-year..	15	7.9- 9.3	8.72		
	F	Adult.....	6	7.8- 8.6	8.12		
		First-year..	10	7.5- 8.7	8.17		
Tarsus	M	Adult.....	16	38.0- 42.7	40.74±0.35	1.41	3.46
		First-year..	17	39.3- 42.8	41.10±0.29	1.19	2.89
		Juvenal....	17	37.3- 43.0	40.35±0.31	1.30	3.22
	F	Adult.....	6	37.5- 39.7	38.80		
		First-year..	12	38.0- 41.2	39.20		
Hind toe	M	Adult.....	16	12.3- 14.2	13.35±0.13	0.54	4.05
		First-year..	16	12.8- 14.8	13.63±0.12	0.50	3.67
		Juvenal....	17	12.3- 14.5	13.34±0.15	0.62	4.65
	F	Adult.....	6	12.3- 13.7	12.97		
		First-year..	12	12.2- 13.5	12.60		
Middle toe	M	Adult.....	16	18.5- 20.8	19.88±0.18	0.71	3.57
		First-year..	16	19.1- 21.7	20.18±0.20	0.80	3.96
		Juvenal....	17	18.8- 20.8	19.78±0.13	0.53	2.68
	F	Adult.....	6	18.0- 20.5	18.95		
		First-year..	12	18.2- 20.1	19.02		
Weights (gm.)	M	15	84 -107	93.4		
	F	9	80 - 89	85.1		

Geographic distribution.—Central coast of California; ranges from southwestern Ventura County (Ojai Valley, Santa Paula) north to southern San Mateo County and Santa Clara County (Los Gatos, San Jose, Calaveras Valley), east to the inner Coast Ranges (Cedar Mountain, in southeastern Alameda County; Mount Hamilton, Santa Clara County; San Benito Mountain, San Benito County; Waltham Creek, Fresno County).

TABLE 7
MEASUREMENTS OF ADULTS OF *A. C. CALIFORNICA* FROM SOUTHERN COASTAL CALIFORNIA
(Santa Barbara and Ventura Counties)

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing.....	M	19	119.0-126.3	122.70±0.55	2.38	1.94
	F	11	114.2-123.0	117.45		
Tail.....	M	18	123.6-142.5	135.72±0.98	4.15	3.06
	F	11	123.1-137.5	128.55		
Bill length.....	M	18	18.3-20.7	19.47±0.17	0.74	3.80
	F	10	17.2-20.2	18.34		
Bill depth.....	M	18	8.2-9.7	9.04±0.09	0.40	4.39
	F	11	8.1-9.0	8.60		
Bill width.....	M	18	7.9-9.7	8.68±0.11	0.47	5.36
	F	11	8.0-9.4	8.70		
Tarsus.....	M	18	37.2-41.4	39.58±0.26	1.12	2.83
	F	11	36.7-41.0	38.73		
Hind toe.....	M	18	12.3-14.1	13.13±0.12	0.53	4.03
	F	11	12.0-13.8	12.61		
Middle toe.....	M	18	18.2-20.8	19.52±0.17	0.73	3.72
	F	10	17.3-19.5	18.85		

Pleistocene fossils of *A. coerulescens* have been found in several areas which border or fall within the southern limits of the race *californica*. These localities are Rancho La Brea, in west Los Angeles (Miller, 1929:7; Howard, 1930), Carpinteria, in southeastern Santa Barbara County (Miller, 1932:173), and McKittrick, in western Kern County (Miller, 1937:250). Scrub jays occur at present at the first two localities, but are absent from the third except possibly as fall or winter vagrants; they were absent also from the Rancho La Brea region, at least as residents, before man-made changes in local habitats. Subspecific identification of these fossil specimens has not been found possible, but careful statistical comparison with recent material yet remains to be made.

Comparisons.—For each subsequent race of the "*californica*" group, the detailed characterization of the race *californica* serves as a basis of comparison. Other than this, comparisons among races are made only with neighboring ones.

Geographic variation and intergradation.—Along the central coast of California, evidence of geographic trends toward races neighboring *californica* is seen primarily in size. To the south, specimens from Santa Barbara and southwestern Ventura counties (table 7) are slightly smaller and represent part of a coastal cline in size (fig. 6). In color they are comparable to specimens from the central

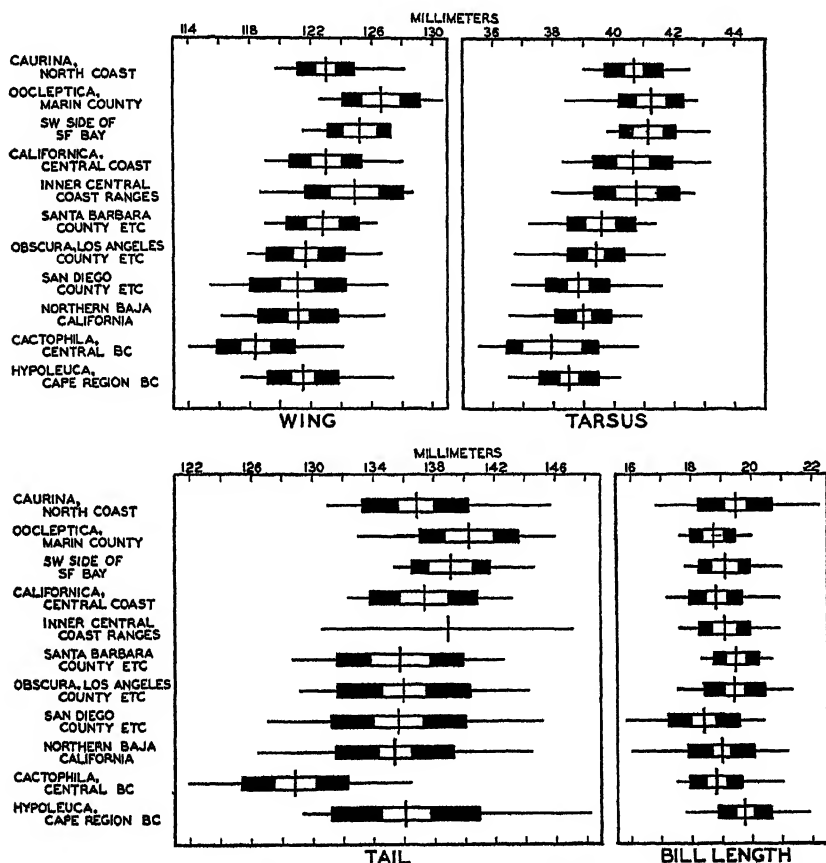


Fig. 6. Individual and geographic variation in races of *Aphelocoma coerulescens* along Pacific coast. Data arranged in north-to-south order except *californica* of inner central Coast Ranges, which is immediately east of central-coast *californica*; data based on adult males.

coast. Farther south and east, in Los Angeles and southwestern San Bernardino counties, intergradation with the southern Californian race *obscura* takes place; relationships with *californica* are described in the discussion of the former race.

Eastward from the central California coast, in Santa Clara County, San Benito County, and the Salinas River drainage of Monterey County, scrub jays are slightly larger than those from the immediate coast in length of wing, tail, bill, and tarsus. (See table 6.) This difference represents a slight shift in range of variation toward the larger birds of the San Joaquin Valley representing the race *superciliosa*; the individual differences are not significant statistically, but they appear

consistently in adult and first-year males, of which adequate samples are available. In color, specimens from San Luis Obispo, eastern Monterey, San Benito, and Santa Clara counties show only a slight tendency toward *superciliosa*, in the absence of dark variants and the presence of pale variants; in the main they are comparable to those from the coast. This tendency is detected chiefly among first-year birds and juveniles, but specimens of these age groups taken along the San Benito-Fresno county line (MVZ 62658, 89767) are clearly comparable to coastal specimens, and the observed duller coloration among first-year birds represents, for the most part, normal age and sex variation seen in other parts of the range of *californica*.

There is little available evidence of intergradation with *superciliosa* along the eastern margin of the range of central-coast *californica*. The western parts of Merced, Fresno, Kings, and Kern counties, where intergradation probably takes place, are represented in series available to me by but six specimens. Two taken near Priest Valley, Fresno County (MVZ 62657, 62658), do not differ from *californica* of adjoining San Benito and Monterey counties. Juvenal specimens collected along the San Luis Obispo-Kern county line (MVZ 93585, 93586, 93588) are clearly *californica* in color. Four taken near McKittrick, Kern County, are closer to *californica* in color than to the duller-colored race occupying the San Joaquin Valley (*superciliosa*), but in measurements they are exceptionally large (wings of adult males, 127.0, 130.8, 132.7 mm.). In color, these specimens represent intergrades; in size, however, they are clearly typical of the larger scrub jays of the San Joaquin Valley. The small series of specimens taken near McKittrick suggests the possibility that northward, in the western foothills of the valley, similar intergradation occurs. In western Stanislaus County (Orestimba Peak), however, scrub jays exhibit color and size characters typical of the central-valley populations; and to the south, on Mount Pinos, this is also true. Two specimens taken south of Mount Pinos (CAS 39785, 39786: head of Piru Creek) are of pale coloration but of smaller size, and represent intergrades between *californica* and *superciliosa* (Swarth 1918:413).

Northward to either side of the southern end of San Francisco Bay, there is relatively abrupt increase in size, and specimens from western Contra Costa and Marin counties are comparable in size range to those from the San Joaquin Valley. In color, however, they do not differ from *californica*. (See p. 223.) Intergradation with the larger jays of the San Francisco Bay region, representing the race *oocleptica*, is clearly seen in the population occupying southeastern San Mateo and northwestern Santa Clara counties (vicinity of Palo Alto) (table 10); in size they are closer to *oocleptica* (table 8) than to coastal *californica* (table 4) and are treated nomenclaturally as part of the former race. They are intermediate between *oocleptica* and interior *californica* (table 6); as described above, however, the larger size of interior *californica* represents a west-to-east trend toward *superciliosa*. This fact, then, has only indirect bearing on the genetic relationships and nomenclatural disposal of birds from the Palo Alto region, since that population immediately adjoins the smaller coastal *californica*. Intergradation probably occurs over western San Mateo and southern Alameda counties, but specimens are lacking. A single adult from southeastern Alameda County (MVZ 56753, Cedar Mountain) is comparable to interior *californica* (wing, 124.6 mm.; tail, 137.8 mm.; tarsus, 40.9 mm.).

Ecologic distribution.—Within the range of *californica* the primary or climax vegetation of the region is that forming the characteristic habitat of scrub jays. Several vegetation types are represented: (1) chaparral associations of *Adenostoma fasciculatum*, *Arctostaphylos* of various species, *Photinia arbutifolia*, *Ceanothus cuneatus*, *Quercus dumosa*, *Q. durata*, *Q. chrysolepis*, *Q. wislizenii*, *Cercocarpus*, and *Rhamnus californica*; (2) other chaparral species of both deciduous and evergreen kinds, such as *Quercus* spp., *Ceanothus* spp., *Arctostaphylos* spp., *Garrya fremontii*, and *Corylus rostrata*, associated with coniferous forests of the Coast Ranges and of local coastal areas such as the Monterey peninsula; (3) woodland associations of oak (*Quercus agrifolia*, *Q. lobata*, *Q. douglasii*, and others), laurel (*Umbellularia californica*), madrone (*Arbutus menziesii*), and buckeye (*Aesculus californica*). The plant communities of this region have been well described by Cooper (1922). Vegetational types of a secondary character which are inhabited by jays are thickets bordering redwood or pine forests (Anderson and Jenkins, 1903:154; Grinnell and Linsdale, 1936:88) and riparian thickets commonly dominated by willows. In the course of a series of brief field excursions to various parts of northern Monterey County in the years 1941–1943 and again in 1947–1948, I have observed scrub jays in these various habitats. Orr (1942:321) lists chaparral and the oak-madrone association as the chief habitats of scrub jays in the Big Basin area of coastal California north of Monterey Bay. In San Benito County, Mailliard (1912:42) found nests of the scrub jay as follows: in oaks, 4; in willows, 8; in chaparral or other shrubs, 6.

Aphelocoma coerulescens oocleptica

Racial characters.—Distinguished from both *californica* and *aurina* by larger size; percentage differences from *californica* in adult males are as follows: wing, +2.9; tail, +2.2; tarsus, +1.5. Wing-tail ratio, 0.902:1. (See table 8 for other statistical data.) Similar to *californica* in color; under tail coverts tinged with pale blue or gray, as in *californica*, but only in approximately 60 per cent of males.

Geographic distribution.—San Francisco Bay region: Marin County and the San Francisco peninsula east and south to southwestern Solano County, central Contra Costa and Alameda counties, and northwestern Santa Clara County.

Near the upper end of the San Francisco peninsula, scrub jays are uncommon or rare locally. According to Mailliard (1930:41), the species was formerly resident in Golden Gate Park, but has become uncommon. It apparently occurs there chiefly as a vagrant, but may nest occasionally (Orr, 1941, MS). It is known to nest at other points on the peninsula. At Lake Merced, for instance, Bolander (1938:22) records the species as a local resident; Hansen and Squires (1917:60) list it as a breeding species in one of the cemeteries of San Francisco. To the south of Lake Merced and San Bruno Mountain, scrub jays are more or less common. Restriction of habitat alone does not adequately explain their rarity in the upper part of the peninsula. Distance between areas of suitable habitat, prevalence of wind-swept fogs, and other unknown factors may impede the normal post-breeding dispersal of scrub jays, so that these areas are reached rarely by several individuals, occasionally by single vagrants, or not at all. Apparently, woodland vegetation occurred in but a few scattered localities on the peninsula before urbanization took place;

TABLE 8
MEASUREMENTS OF *A. C. OOCLEPTICA* FROM MARIN COUNTY, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	16	122.6-130.7	126.62±0.64	2.58	2.04
		First-year..	26	110.2-128.4	124.08±0.43	2.18	1.76
	F	Adult.....	18	117.6-125.0	121.17±0.49	2.09	1.72
		First-year..	22	114.5-123.8	119.64±0.52	2.42	2.03
Tail	M	Adult.....	16	133.0-146.0	140.31±0.82	3.28	2.33
		First-year..	26	127.8-140.5	135.15±0.74	3.78	2.80
	F	Adult.....	17	123.7-140.0	131.53±0.98	4.07	3.09
		First-year..	20	122.9-136.6	129.00±0.72	3.22	2.49
Bill length	M	Adult.....	17	17.6- 20.0	18.74±0.18	0.74	3.95
		First-year..	18	16.6- 20.4	18.78±0.24	1.00	5.31
	F	Adult.....	17	16.6- 20.2	18.28±0.26	1.07	5.86
		First-year..	18	16.1- 19.3	17.57±0.21	0.89	5.07
Bill depth	M	Adult.....	17	8.6- 10.1	9.36±0.10	0.42	4.49
		First-year..	18	8.5- 9.9	9.34±0.08	0.35	3.73
	F	Adult.....	16	8.5- 9.8	9.05±0.10	0.39	4.29
		First-year..	18	8.4- 9.5	8.87±0.08	0.32	3.60
Bill width	M	Adult.....	17	8.2- 9.5	8.90±0.08	0.33	3.66
		First-year..	18	8.0- 9.3	8.86±0.07	0.30	3.34
	F	Adult.....	17	7.8- 9.2	8.66±0.08	0.34	3.93
		First-year..	18	8.2- 9.2	8.71±0.06	0.27	3.15
Tarsus	M	Adult.....	17	38.4- 42.8	41.24±0.26	1.07	2.60
		First-year..	21	38.7- 44.2	41.90±0.31	1.43	3.45
	F	Adult.....	18	36.9- 42.5	40.17±0.29	1.24	3.08
		First-year..	22	37.5- 41.9	40.15±0.22	1.05	2.61
Hind toe	M	Adult.....	17	12.5- 14.5	13.68±0.12	0.51	3.73
		First-year..	21	12.0- 14.8	14.06±0.13	0.58	4.11
	F	Adult.....	18	12.9- 14.5	13.59±0.11	0.47	3.47
		First-year..	22	12.6- 14.2	13.30±0.08	0.39	2.91
Middle toe	M	Adult.....	17	19.5- 21.1	20.38±0.10	0.40	1.96
		First-year..	21	19.5- 22.2	20.87±0.17	0.79	3.79
	F	Adult.....	18	18.7- 20.0	19.98±0.14	0.58	2.89
		First-year..	22	18.9- 20.6	19.70±0.08	0.37	1.86
Weights (gm.)	M	7	90 -110	100.4		
	F	2	90 -107	98.5		

Golden Gate Park, for instance, was part of an extensive sand-dune area (Hansen and Squires, 1917:56).

"Aphelocoma californica" has been reported by Gruber (1884:172) as a vagrant on the Farallon Islands, which are about thirty miles west of the Golden Gate and fifteen miles from the nearest part of the mainland, Point Reyes to the north. The

TABLE 9

MEASUREMENTS OF *A. C. OOCLEPTICA* FROM CONTRA COSTA AND ALAMEDA COUNTIES, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	21	123.1-131.5	126.29±0.51	2.34	1.85
		First-year..	27	119.5-129.4	123.59±0.52	2.68	2.17
	F	Adult.....	21	118.7-126.9	122.19±0.53	2.44	2.00
		First-year..	21	112.9-124.4	119.09±0.66	3.04	2.55
Tail	M	Adult.....	20	132.8-146.1	141.10±0.82	3.68	2.60
		First-year..	27	128.4-141.8	134.37±0.59	3.06	2.28
	F	Adult.....	21	128.9-141.3	133.62±0.68	3.14	2.35
		First-year..	20	124.5-138.7	129.90±0.81	3.63	2.80
Bill length	M	Adult.....	20	18.2- 20.9	19.22±0.18	0.79	4.12
		First-year..	15	17.3- 21.8	18.94±0.25	0.97	5.13
	F	Adult.....	21	16.2- 19.5	18.35±0.19	0.87	4.74
		First-year..	15	15.9- 19.3	17.82±0.25	0.96	5.39
Bill depth	M	Adult.....	18	9.0- 10.1	9.56±0.08	0.32	3.37
		First-year..	14	9.0- 9.8	9.35		
	F	Adult.....	21	8.3- 9.9	9.05±0.09	0.40	4.37
		First-year..	15	8.3- 9.6	8.86±0.09	0.34	3.83
Bill width	M	Adult.....	21	8.4- 9.7	9.02±0.07	0.34	3.77
		First-year..	15	8.2- 9.6	8.89±0.09	0.36	4.05
	F	Adult.....	21	8.0- 9.2	8.53±0.07	0.31	3.66
		First-year..	15	7.9- 8.9	8.36±0.08	0.29	3.50
Tarsus	M	Adult.....	21	39.2- 44.4	41.56±0.27	1.22	2.93
		First-year..	27	38.3- 43.3	41.20±0.19	0.97	2.36
	F	Adult.....	21	37.8- 42.9	40.58±0.28	1.27	3.13
		First-year..	22	37.5- 42.1	39.89±0.27	1.28	3.22
Hind toe	M	Adult.....	21	12.9- 14.8	13.90±0.13	0.59	4.23
		First-year..	27	12.4- 15.6	13.77±0.11	0.58	4.25
	F	Adult.....	21	12.2- 14.4	13.53±0.13	0.58	4.25
		First-year..	22	12.6- 14.2	13.29±0.11	0.54	4.06
Middle toe	M	Adult.....	21	18.8- 21.8	20.46±0.16	0.76	3.80
		First-year..	27	19.0- 22.0	20.30±0.12	0.62	3.08
	F	Adult.....	20	18.8- 20.9	19.74±0.13	0.59	3.00
		First-year..	22	18.5- 21.3	19.68±0.13	0.63	3.20
Weights (gm.)	M	7	100 -112	105.9		
	F	9	80 -101	93.4		

date of observation is lacking from the report. But the record is of special significance in that it is the only evidence, to my knowledge, bearing upon the questioned ability of scrub jays to fly across a large expanse of water. (See p. 272.)

Comparisons.—*Oocleptica* is similar to, or slightly larger than, *superciliosa* of the Sacramento and San Joaquin valleys. (See pp. 256-261 for details.) It is dis-

TABLE 10

MEASUREMENTS OF *A. C. OOCLEPTICA* FROM SOUTHWESTERN SAN MATEO AND NORTHWESTERN SANTA CLARA COUNTIES, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	13	121.5-127.2	125.23±0.57	2.05	1.64
		First-year..	28	116.7-126.6	122.64±0.49	2.58	2.10
	F	Adult.....	10	114.6-124.4	119.00		
		First-year..	14	113.8-121.7	117.93		
Tail	M	Adult.....	13	135.4-144.6	139.08±0.72	2.62	1.88
		First-year..	25	127.6-140.0	134.52±0.60	2.99	2.22
	F	Adult.....	10	123.7-135.0	128.40		
		First-year..	13	121.8-133.6	128.00		
Bill length	M	Adult.....	13	17.8- 21.0	19.11±0.23	0.84	4.38
		First-year..	29	17.4- 20.3	18.97±0.13	0.70	3.70
	F	Adult.....	9	16.9- 19.2	18.03		
		First-year..	15	17.0- 19.7	18.24		
Bill depth	M	Adult.....	12	9.4- 10.0	9.67±0.07	0.23	2.38
		First-year..	29	8.6- 10.4	9.33±0.07	0.40	4.26
	F	Adult.....	9	8.4- 9.5	9.01		
		First-year..	15	8.2- 9.7	8.92		
Bill width	M	Adult.....	13	8.0- 9.7	9.02±0.14	0.51	5.65
		First-year..	29	8.4- 10.2	9.08±0.08	0.43	4.74
	F	Adult.....	7	7.7- 9.0	8.36		
		First-year..	15	7.8- 9.4	8.60		
Tarsus	M	Adult.....	13	39.8- 43.2	41.14±0.26	0.93	2.27
		First-year..	29	39.5- 43.7	41.66±0.21	1.13	2.70
	F	Adult.....	10	37.1- 42.6	39.86		
		First-year..	15	38.8- 41.5	40.30		
Hind toe	M	Adult.....	12	12.2- 14.3	13.30±0.18	0.61	4.56
		First-year..	28	12.6- 14.5	13.62±0.08	0.43	3.15
	F	Adult.....	10	12.6- 13.7	13.20		
		First-year..	15	12.5- 13.8	13.30		
Middle toe	M	Adult.....	12	18.7- 21.2	20.30±0.20	0.71	3.53
		First-year..	28	19.3- 21.5	20.13±0.10	0.51	2.53
	F	Adult.....	11	17.5- 20.4	19.35		
		First-year..	13	18.9- 20.5	19.62		

tinguished from that race by darker coloration. Blue areas are more purplish, the back is less gray, under parts are lighter, and under tail coverts are less frequently white. These differences parallel those between *californica* and *superciliosa*.

Oocleptica differs from *caurina* in size to approximately the same degree as it does from *californica* (see above); although in figure 6 it is shown that the bill is intermediate in *oocleptica* between *caurina* (the larger) and *californica* (the

smaller), this difference does not appear consistently in all age groups and sex classes and is probably insignificant. In *oocleptica*, blue areas are less purplish and the back is lighter and less gray than in *caurina*; these color distinctions, however, are not so strong as similar ones between *caurina* and *californica*, since *oocleptica* is merely a segment in a coastal color cline. (See p. 225.)

Geographic variation and intergradation.—Specimens from Marin County are comparable in color to *californica* except that in series a more purplish cast is apparent in several specimens. In this respect they are part of a clinal trend which reaches a maximum in northernmost populations of *caurina*. Increasingly purplish-blue coloration is also seen in specimens from the east side of San Francisco Bay (Berkeley and Oakland), although one specimen (RE 2275) suggests the valley race *superciliosa* in the absence of purplishness on head and sides of chest. East of the Berkeley Hills as well as southward, at Hayward, size remains comparable to both previously mentioned populations of *oocleptica* (see tables 8 and 9), but color becomes paler, a trend representing intergradation with *superciliosa* to the east. At Hayward, just south of Oakland on the east shore of San Francisco Bay, variability in color ranges from the richest purplish blue (CAS 23083) to be seen in *oocleptica* of Marin County to a duller, less purplish shade (CAS 48259) approaching that of *superciliosa*. In general, specimens from these areas are preponderantly of the latter type, but this is more true of adult males than of adult females; in other words, females suggest intergradation with *superciliosa* less than do males, and are closer to coastal populations in color than are males. Among juvenal specimens, those representing the area east of the Berkeley Hills (Moraga and Walnut Creek) tend toward *superciliosa* in paling (graying) of head and back, but they are intermediate or more similar to *californica*; and in color of wings and tail they are closer to *californica*. Intergradation between *oocleptica* and *superciliosa* occurs also in southwestern Solano County (see p. 227); it continues in the eastern half of Contra Costa County (Mount Diablo, Nortonville, Somersville), but specimens of both adults (RE 2675, MVZ 89425) and juveniles (MVZ 22758, 22759) are closer to *superciliosa*. Specimens from central Solano County (Vacaville) are also referable to *superciliosa*; one juvenile (see p. 227), however, closely approaches *oocleptica-californica* in color and is darker than the above-mentioned specimens from Moraga and Walnut Creek. Thus the area of intergradation between *oocleptica* and *superciliosa* appears to be a broad belt almost as large as the area over which "typical" *oocleptica* occurs.

Intergradation with *californica* has been discussed. (See p. 218.)

Ecologic distribution.—The habitats of scrub jays of the race *oocleptica* do not differ significantly in floral character from those of *californica*. In Marin County these are the redwood-border forests of broad-leaved trees such as madrone, oak, and laurel together with local woodlands of pine (*Pinus muricata*) or broad-leaved trees adjoining or mixed with chaparral. The distribution of 83 nests found by Mailliard (1912:42) in Marin County was as follows: oak, 69; laurel, 3; *Rhamnus californica*, 4; elder, 2; *Rhus diversiloba*, 2; madrone, 1; toyon (*Photinia arbutifolia*), 1; *Ribes*, 1.

Around San Francisco Bay and inland eastwardly, habitats of scrub jays differ only in that the redwood-border forest is much restricted and, for the most part,

absent. In the Berkeley Hills, scrub jays have been recorded by me chiefly in woodlands of oak, laurel, buckeye with poison oak, hazel, elder, *Holodiscus*, *Baccharis*, *Photinia*, and *Rubus* as prominent understory or border shrubs; they occur somewhat less frequently in broken chaparral, here composed chiefly of *Baccharis*, but including also *Rhamnus*, *Artemisia*, *Lupinus*, *Eriodictyon*, and *Diplacus* as co-dominants. The species is especially abundant locally where woodland areas adjoin chaparral-covered slopes or ridges. Nests have been located most frequently in oaks, but also in willows and poison-oak thickets. Stoner (1921:95) found three nests in buckeyes on the south side of Carquinez Strait. In areas overgrown with introduced trees and shrubs, scrub jays have been observed nesting in dense, peripheral foliage of pine and cypress, and in an ivy-covered almond tree, and in *Pyracantha* shrubs. Stoner (1932:365) observed nests of *oocleptica* placed in thickets of mistletoe (*Phoradendron villosum*), parasitic chiefly on oaks.

Tomaes Point, forming the northwestern corner of Marin County, is covered with a scattered maritime brush in which *Lupinus* is prominent. This shrubby cover, even with occasional islands of planted eucalyptus and cypress trees, is generally too low and open to offer adequate cover for scrub jays. The species is not common, and the records from Tomaes Point may represent intermittent invasion of the area from the south rather than a resident population of normal density.

Along the Pacific coast at the Marin-Sonoma county line and extending inland several miles is a belt of open country, used at present chiefly as grazing land, over which there are only small, local areas of thickets. I examined much of this region during a six-week period spent in residence at Dillon Beach, Marin County, at the lower end of Bodega Bay, in the spring of 1941. Scrub jays were recorded at that time only on Tomaes Point and, to the north of the belt described here, one mile east of Bodega Lagoon. Inland, from ten to fifteen miles from the coast, thence to the east side of the Marin peninsula and the Petaluma River drainage, habitat suitable for scrub jays becomes increasingly common. Much of the area west of Petaluma is grazed or farmed, however, and the clearing of the land may have enlarged any expanse of originally open country. In any event, the area acts as a local barrier, the effectiveness of which is reflected in rather striking differences of size between scrub jays to the north and south.

Little information is available in regard to the history of the vegetation of this belt of open country. It is known, however, that islands of upland, shrub, or forest vegetation, which might be interpreted as remnants of an original extensive plant cover, have not been so identified, or even located. The possibility that coniferous forest, even of partially developed character, covered the coast to the east and south of Bodega Bay remains doubtful. So far as known now, the area, before man's entry of it, seems to have been a grassland barren of the type to be seen in other local areas along the central coast of California. Locally, along streams, thickets are present, but because they are too restricted, or too distantly removed from each other, or are otherwise inadequate in the absence of adjoining upland chaparral or woodland, scrub jays are uncommon or absent. Since the species is present to the north as well as the south in regions of comparable climate, it appears that biotic and primarily vegetational factors account for its restricted occurrence there.

***Aphelocoma coerulescens caurina*, new subspecies**

Type.—Adult male, no. 97715, MVZ; one mile east of Wedderburn, 50 feet, Curry County, Oregon, October 10, 1947; collected by Ward C. Russell, orig. no. 10663.

Racial characters.—Color most similar to that of *californica* and *oocleptica*, thus darker than *immanis* or *superciliosa*; compared to *californica* and *oocleptica*, blue areas of a more purplish hue, especially on head and pileum, and slightly brighter (closest to Deep Dull Violaceous Blue); back darker and more gray (less brown, nearest to Fuscous); in six of eleven adult males, breast washed with Smoke Gray, thus darker than in *californica* or *oocleptica* and suggesting the race *obscura*. Similar to *A. c. californica* in size, thus smaller than *oocleptica*, *superciliosa*, and *immanis*. Wing-tail ratio, 0.899:1. (See table 11 for other statistical data.)

Geographic distribution.—Coast of southwestern Oregon and northern California, from Curry County (Wedderburn) south to Sonoma County (Petaluma, Sonoma) and Napa County (Mount Veeder) and east to the inner Coast Ranges (Hayfork Basin, Trinity County; Clear Lake, Lake County; Howell Mountain, Napa County).

If scrub jays occur farther north, beyond the valley of the Rogue River, along the northern shore of which Wedderburn is located, they probably do so for only about ten or fifteen miles. At that distance the coastal forests of conifers become more or less continuous, and habitat extensive enough to support a population is not available.

Comparisons.—For comparison of *caurina* with *oocleptica* see page 222. For comparison of *caurina* with *superciliosa* see discussion of intraracial variation under latter race.

Geographic variation and intergradation.—A cline in color of blue areas occurs in coastal populations from Santa Barbara and San Luis Obispo counties northward to Curry County in southwestern Oregon. It passes gradually, without evident interruption, through *californica*, *oocleptica*, and *caurina*, and is detectable only through comparisons of series of specimens of comparable sex and age groups from these coastal areas. The geographic extremes are clearly distinguishable from each other.

Besides the change in color of blue areas, the back becomes slightly darker northward. The breast in six of eleven adult males from Wedderburn, Oregon, is washed with Smoke Gray, and is thus darker than in populations of *californica* and *oocleptica* to the south. Under tail coverts of north-coast males, from Del Norte County, California, southward, are tinged in about 50 per cent of specimens. However, the ratio may shift northwardly; in eight of eleven adult males from Curry County, under tail coverts are tinged.

These several tendencies indicate that the cline in color of blue areas is accompanied by correlated tendencies toward darkening in color of back and under parts. In size, however, populations from Sonoma County northward are comparable to *californica* of Santa Cruz and Monterey counties.

Under these conditions it may be expected that populations of medium-sized individuals to the north and south of the large coastal race *oocleptica* are indistinguishable, and this holds true. From Humboldt County southward, purplish variants characteristic of the northern part of the range of *caurina* become fewer and fewer; the southernmost record of a dark purplish variant comparable to the

TABLE 11
MEASUREMENTS OF *A. C. CAURINA* FROM NORTHERN COASTAL CALIFORNIA
AND SOUTHWESTERN OREGON

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	38	119.7-128.2	123.00±0.32	1.88	1.53
		First-year..	25	117.0-126.1	121.84±0.50	2.51	2.06
	F	Adult.....	29	114.6-122.5	119.00±0.41	2.23	1.87
		First-year..	32	113.0-122.2	116.84±0.42	2.38	2.04
Tail	M	Adult.....	36	131.0-145.7	136.83±0.59	3.54	2.59
		First-year..	25	125.0-144.1	133.88±0.94	4.71	3.53
	F	Adult.....	28	125.0-137.7	131.11±0.60	3.18	2.42
		First-year..	31	120.0-131.7	125.71±0.58	3.21	2.56
Bill length	M	Adult.....	41	16.8- 22.3	19.48±0.19	1.23	6.31
		First-year..	22	18.2- 21.4	19.30±0.18	0.83	4.31
	F	Adult.....	30	16.6- 20.2	18.36±0.17	0.96	5.25
		First-year..	24	16.8- 19.9	18.17±0.16	0.78	4.28
Bill depth	M	Adult.....	41	8.9- 10.0	9.42±0.05	0.29	3.12
		First-year..	22	9.0- 10.1	9.42±0.06	0.27	2.90
	F	Adult.....	30	8.2- 9.7	8.97±0.06	0.33	3.65
		First-year..	24	8.4- 9.9	8.95±0.07	0.36	3.98
Bill width	M	Adult.....	41	8.0- 9.9	8.98±0.07	0.44	4.86
		First-year..	21	8.0- 9.5	9.03±0.07	0.33	3.61
	F	Adult.....	30	8.0- 9.6	8.59±0.07	0.38	4.44
		First-year..	24	7.8- 9.1	8.58±0.07	0.36	4.23
Tarsus	M	Adult.....	39	39.0- 42.5	40.66±0.16	0.97	2.39
		First-year..	28	38.2- 43.6	41.19±0.22	1.17	2.84
	F	Adult.....	30	36.6- 42.7	39.82±0.25	1.35	3.39
		First-year..	34	36.9- 41.6	39.68±0.17	1.02	2.57
Hind toe	M	Adult.....	41	12.6- 14.6	13.58±0.07	0.44	3.23
		First-year..	28	12.5- 14.5	13.77±0.09	0.48	3.50
	F	Adult.....	29	12.4- 14.4	13.11±0.09	0.49	3.77
		First-year..	34	12.1- 14.1	13.12±0.08	0.46	3.54
Middle toe	M	Adult.....	41	19.1- 21.3	20.14±0.10	0.65	3.23
		First-year..	28	18.6- 21.7	20.48±0.14	0.72	3.53
	F	Adult.....	29	18.3- 20.8	19.65±0.12	0.63	3.21
		First-year..	34	18.0- 20.9	19.29±0.09	0.53	2.76
Weights (gm.)	M	29	87 -111	98.4		
	F	9	80 - 97	87.7		

extreme reached in Curry County is one specimen from Santa Cruz County (MVZ 72591, Bonnie Doon). Specimens from Mendocino and Sonoma counties along the northern California coast are not distinguishable in series, at least so far as available material indicates, from those of Santa Cruz and Monterey counties.

Differences separating north-coast and central-coast populations thus result from slight clinal shifts in several color characters northward, the most marked of which is increased purplishness of blue areas. Although southern populations of *caurina* cannot be separated satisfactorily for nomenclatural purposes from northern populations of *californica*, they are obviously not to be regarded as genetically identical, or even more closely related to each other than to *oocleptica* or *superciliosa*.

Intergradation between *caurina* and the adjoining races *oocleptica* and *superciliosa* mirrors in part the relationships of *californica* to these two races. The coastal cline in size shifts even more abruptly near the northern limits of the San Francisco Bay region than along the northern limits of central-coast *californica*. Apparently, interbreeding of *oocleptica* with *caurina* along the immediate coast is hindered or prevented by the relatively treeless belt of southern Sonoma and extreme northern Marin counties. Intergradation might be expected in southeastern Sonoma County, but available specimens are small and comparable to *caurina*. For example, an adult female from Sonoma (MVZ 33786) measures as follows (mm.): wing, 115.6, tail, 127.4; bill length, 16.8; tarsus, 39.8. In specimens from southeastern Solano County, color characters are mixed; shades of blue on head represent the lighter-colored race of the valley (*superciliosa*) and coastal populations (*oocleptica*) as well; in size (mm.) a wide range of variation also occurs (wings of adult males, 121.2–133.5; of females, 119.6–126.0). These specimens from Solano County appear to me closer to *oocleptica* and are so treated here, but they are best regarded as representatives of an area of geographic contact between three different races. Others, taken three miles west of Vacaville in Solano County, are pale and clearly referable to *superciliosa*; one, however, a juvenal specimen (MVZ 22752), is distinctly darker and provides additional evidence of intergradation within the same area of contact.

Evidence of intergradation eastward with populations occupying south-central Oregon, north-central California, and the Sacramento Valley is limited and, in the last-mentioned area, vague. In the northern part of the zone of contact between *caurina* and *superciliosa* the line of separation remains arbitrary until more specimens are available. Presumably, intergradation takes place over a fairly broad belt, interrupted extensively by areas of coniferous forest in the region of the Klamath Mountains. In southern Oregon, where *caurina* adjoins an area of intergradation between *superciliosa* of the Sacramento Valley and regions to the east and south, and another race to the north, *inmanis* of the Willamette Valley, dark variants become inseparable from coastal specimens on the basis of color; but a significant size differential exists between jays from south-central Oregon and those from the immediate coast, the latter being smaller; moreover, in series the more purplish coloration of the coastal population can also be seen.

Southward, the area of intergradation between *caurina* and *superciliosa* is a broad belt along either side of the crest of the inner Coast Ranges extending into Napa County. This is not a belt of intergradation in the sense that specimens from it represent intermediates between *californica* and *superciliosa*. The situation is complicated by the fact that scrub jays of the Sacramento Valley are especially variable in characters, of color and size of wing and tail; they may overlap or

entirely span the range of variation of *caurina*. Comparison of tables 17 and 11 reveals that in wing and tail measurements the coastal race is better regarded as a segregate of the more variable populations of the valley. The two do not differ in size of bill and foot or in average weight. In color, coastal specimens are darker about the head and chest and less gray on the back, but in these characters there is probably an overlap of 30 to 40 per cent between coastal specimens and those of the Sacramento Valley. Thus the coastal populations differ chiefly in having darker coloration and shorter wings and tails; those of the Sacramento Valley constitute a part of the race *superciliosa* in which the characters of that race are poorly developed. This situation is analyzed in detail on page 256; suffice it to state here that because of a preponderance of large and (or) pale variants, jays of the Sacramento Valley are placed with the race *superciliosa*. It would follow, then, that the line of separation between *caurina* and *superciliosa* might best rest on the presence of specimens displaying any of these characters along the zone of contact; since I have seen but two such specimens taken west of the inner Coast Ranges (Clear Lake area), the line has been placed along the crest of these mountains.

Adult specimens from the Hayfork Basin, while worn, appear darker than specimens of comparable age and wear from the Sacramento Valley and most similar to those from the coast. In size, adult males suggest a slight shift toward the larger valley race, but remain within the range of variation of coastal populations. One juvenile from the same locality (MVZ 88451) is as dark as the darkest variants of *caurina*. Specimens from Beegum, in the Sacramento River drainage, are paler than others of comparable wear from Trinity and Humboldt counties; in size, the former are similar to smaller variants of the Sacramento Valley and do not differ from the coastal race. Specimens from the Hayfork Basin are placed with *caurina*; those from Beegum, with *superciliosa*. Jays from the Clear Lake region, Lake County, to the south, have been placed by Swarth and other investigators with the valley race "*immanis*" (= *superciliosa*). On the basis of the evidence and criteria discussed above, I would place all specimens examined by me with *caurina*, for, with one or two exceptions, none shows clearly any characters of, or signs of intergradation toward, *superciliosa*. One lighter adult male from Castle Hot Springs (CAS 23630) is similar to others taken closer to the coast (for example, MVZ 81289, Laytonville). Another, a first-year male taken five miles east of Upper Lake, does not differ in color from first-year males of *caurina*, and suggests intergradation with *superciliosa* only in that it is larger than averaged-sized specimens of *caurina*. Several adult females in fresh fall plumage from southern Lake County (CAS 20300, 20215, 23632) are similar in size to specimens from the immediate north coast (Mailliard, 1919:296). One (20300) is paler than the others in color of both head and back, and may be regarded as an intergrade. An adult male from central Napa County (MVZ 83275, Angwin) is clearly referable to the coastal race on the basis of size and color.

Several authors (for example, Mailliard, 1908:133; Swarth, 1918:414) have described a tendency of certain passerines, as *Thryomanes*, *Psaltiriparus*, and *Cyanocitta*, from Sonoma County to resemble in racial characters the neighboring valley races of the respective species. Swarth (1918:415) states that a similar tendency toward paleness is seen in *Aphelocoma*, but the specimens upon which,

I believe, he based his statements in the main are four females (all in the Museum of Vertebrate Zoölogy), which, because they are first-year birds, are duller and paler than adults, but not more so than other first-year females of *caurina*. Since Swarth did not, so far as I can determine, differentiate first-year and adult birds, his statement is understandable. One adult male (CAS 33584) taken in northern Sonoma County is perceptibly less purplish than most adult males from the coast, but it does not fall out of the range of normal variation. More suggestive of any tendency toward the valley race are specimens of four juvenal birds from Sonoma County (all in MVZ, Guerneville); whereas other juveniles of *caurina* which I have examined are comparable to those of *californica*, these four are lighter in color, with more gray above and paler blue suffusion of the crown area.

Ecologic distribution.—Along the northern coast of California, scrub jays are distributed according to the occurrence of secondary communities of shrubs and broad-leaved trees in disturbed areas, along streams, and in physiographically varied areas, where the coniferous forest is only partially developed, interrupted, or absent. They have been reported, for example, associated with growths of poison oak (*Rhus diversiloba*) and buckeye (Mailliard, 1916:199), and with groves of young oaks (*Quercus garryana*) (Fisher, 1904:51). On Howell Mountain in central Napa County, Hemphill (1944, MS) found scrub jays chiefly in areas of woodland adjoining or mixed with chaparral, but also in black oaks (*Q. kelloggii*) and manzanita (*Arctostaphylos manzanita*) associated with yellow pines (*Pinus ponderosa*). To the north, in the Hayfork Basin, Trinity County, scrub jays were observed by me in June, 1943, chiefly in open woodland association of oak (*Q. kelloggii*, *Q. garryana*) and yellow pine interspersed with shrubs of moderate height, chiefly *Ceanothus* and *Arctostaphylos*. At Hyampom, near the Trinity-Humboldt county line, scrub jays were present in mixed vegetation of pine, oak, fir (*Pseudotsuga taxifolia*), and various shrub species, as *Quercus chrysolepis*, *Cercocarpus betuloides*, *Prunus subcordata*, *Cercis occidentalis*, *Rhus trilobata*, *Rhamnus californica*, and *Arctostaphylos manzanita*; they were noted to wander from this habitat into near-by groves of willow (*Salix melanopsis*) and poplar (*Populus trichocarpa*) along the Trinity River. Toward the coast and northward, areas of suitable habitat within the expanses of coniferous forest become increasingly restricted. Scrub jays occur over much of this area only in isolated colonies, and are known to occur similarly northward into Curry County in southwestern Oregon.

Field investigations in the region of Wedderburn, Curry County, at the mouth of the Rogue River, in October, 1947, revealed that scrub jays occur there mainly in the broken vegetation of the open, south-facing slopes of the river valley. The higher, more exposed slopes, hill crests, and alluvial flats within a few miles of the ocean shore are for the most part cultivated or grazed. When undisturbed, the upland sites, at least within one or two miles of the ocean, are covered with a dense, low growth of salal (*Gaultheria shallon*), *Ceanothus*, *Baccharis*, other shrubs, ferns, and tall herbs. Mixed forest and shrub vegetation fills the draws and spreads to adjacent slopes. The forests consist mainly of Douglas fir (*Pseudotsuga taxifolia*) and broad-leaved trees (chiefly *Lithocarpus densiflora*, *Arbutus menziesii*, *Acer macrophyllum*, and *Umbellularia californica*). Chaparral-like areas are dominated chiefly by *Corylus*, intermixed with *Symphoricarpos*, *Rubus*, *Rosa*, and *Rhus*

diversiloba, together with a fern (*Polystichum*) growing everywhere beneath and among the shrubs. Along streams, various of these shrubs are intermixed with willows and alders.

Along the borders of forests or about groves of trees wherever a rather extensive shrub cover occurs, or in the vicinity of stream-border thickets of tall shrubs adjacent to open ground, scrub jays are present. Large islands of shrubbery in draws where broken, tall growths of alders and willows or scattered, tall conifers, or both occur, form an especially preferred habitat. Close to the coast, jays are present about extensive thickets of azalea (*Rhododendron occidentale*), cascara (*Rhamnus purshiana*), and other shrubs in the vicinity of groves of *Pinus contorta*.

The habitat of scrub jays in this region does not differ in essential features from that of *occidentalis* near Berkeley, California, or *californica* near Monterey. In the period of my observation at Wedderburn, October 7–11, scrub jays were not common, but they occurred regularly in areas of suitable habitat. Steller jays were more numerous and in part overlapped with scrub jays in habitat distribution; both occurred in the vicinity of thickets bordering forest islands or in open groves of conifers.

Aphelocoma coerulescens obscura

Racial characters.—Compared with *californica*, averages darker; pileum, hind neck, and sides of neck and chest more purplish (darker than Deep Dull Violaceous Blue, tending toward Indulin Blue—Cyanine Blue); back more brownish (Fuscous—Hair Brown), rarely with any bluish suffusion; throat more heavily and darkly streaked with gray; sides of throat darker (more purplish, as above); mid-feathers of upper breast forming collar edged with more blue and gray; upper breast, belly, and sides washed with more smoky gray brown (Smoke Gray to Light Drab), a difference best seen on the sides, which become Light Drab; dull white area on lower belly more restricted; under tail coverts more frequently tinged with blue (approximately 80 per cent of adult males) and averaging darker than in *californica* (reaching Pale Windsor Blue or Dutch Blue); ankle feathers darker (Mouse Gray to Deep Mouse Gray), tinged with dull blue in approximately 75 per cent of adult males; rectrices and remiges of slightly brighter blue (approaching Grayish Violaceous Blue). In size, smaller than *californica*; percentage differences in adult males are as follows: wing, -1.5 ; tail, -1.4 ; bill length, $+1.0$; tarsus, -4.1 . Wing-tail ratio, $0.895:1$. (See table 12 for other statistical data.)

Juvenal plumage comparable to or slightly darker than that of *californica*; dorsum appears browner (less gray) in occasional variants; belly and ankle feathers may be washed with more pale brownish gray.

Geographic distribution.—Southwestern California, from the San Gabriel, San Bernardino, and San Jacinto mountains southward into Baja California, along the Coast Ranges to the lower end of the Sierra San Pedro Mártir; thence westward to the Pacific coast from Los Angeles County south to Ensenada (Todos Santos Bay).

In Riverside County, *obscura* is limited eastwardly by the Coachella Valley, but it occurs beyond this local barrier along the tongue of woodland and chaparral found on the Little San Bernardino Mountains at least as far as Pinyon Wells. North of this locality scrub jays range eastward to the vicinity of Twentynine Palms.

One record of a first-year female (MVZ 59581) taken at San Fernando (1,100 feet), Baja California, on January 5, 1931, falls considerably south of the known breeding range of *obscura* (see fig. 5) and represents a straggler. Two scrub jays

TABLE 12
MEASUREMENTS OF A. C. OBSCURA FROM NORTHERN BAJA CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	56	116.1-126.8	121.16±0.35	2.63	2.16
		First-year..	20	115.6-123.6	119.75±0.50	2.24	1.87
	F	Adult.....	28	112.2-122.3	116.57±0.47	2.50	2.14
		First-year..	17	111.5-117.8	114.24±0.51	2.10	1.84
Tail	M	Adult.....	53	126.4-144.4	135.36±0.54	3.90	2.88
		First-year..	20	124.0-141.0	131.80±1.04	4.65	3.53
	F	Adult.....	24	118.5-136.4	128.71±0.89	4.35	3.38
		First-year..	15	116.7-128.5	122.60		
Bill length	M	Adult.....	51	16.0- 21.2	18.98±0.15	1.09	5.75
		First-year..	22	16.2- 19.5	18.44±0.15	0.72	3.90
	F	Adult.....	27	15.5- 20.0	17.75±0.19	1.01	5.68
		First-year..	12	16.1- 19.6	17.60		
Bill depth	M	Adult.....	50	8.0- 9.2	8.57±0.05	0.32	3.79
		First-year..	21	7.7- 9.0	8.48±0.08	0.36	4.21
	F	Adult.....	25	7.6- 8.7	8.10±0.06	0.28	3.40
		First-year..	11	7.6- 8.3	7.88		
Bill width	M	Adult.....	53	7.3- 9.3	8.22±0.06	0.45	5.47
		First-year..	21	7.6- 8.6	8.09±0.06	0.29	3.53
	F	Adult.....	28	7.3- 8.6	7.86±0.06	0.31	3.95
		First-year..	11	7.2- 8.3	7.76		
Tarsus	M	Adult.....	50	36.5- 40.9	38.97±0.13	0.94	2.42
		First-year..	21	37.5- 40.8	38.95±0.18	0.83	2.14
	F	Adult.....	29	34.7- 39.8	37.70±0.21	1.12	2.96
		First-year..	17	36.1- 39.0	37.40±0.20	0.81	2.16
Hind toe	M	Adult.....	53	12.0- 14.0	12.76±0.07	0.51	3.97
		First-year..	22	12.1- 13.9	12.70±0.10	0.46	3.59
	F	Adult.....	29	11.4- 13.0	12.28±0.08	0.41	3.33
		First-year..	17	10.9- 12.9	12.01±0.14	0.59	4.91
Middle toe	M	Adult.....	52	17.0- 20.0	18.70±0.09	0.68	3.66
		First-year..	22	17.5- 19.9	18.87±0.13	0.63	3.33
	F	Adult.....	27	17.0- 19.8	18.20±0.11	0.58	3.19
		First-year..	17	16.4- 19.1	17.73±0.15	0.63	3.55
Weights (gm.)	M	51	70 - 93	78.2		
	F	23	59 - 76	69.7		

observed by Huey (1926:355) at Santo Domingo on February 21, 1925, also represent stragglers. Along the eastern bases of the Coast Ranges north to the Mojave Desert, local wandering to elevations below the breeding habitat probably takes place, but records are lacking. Four specimens (all in the Museum of Vertebrate Zoölogy) taken near the San Bernardino-Riverside county line east of the San

TABLE 13

MEASUREMENTS OF *A. C. OBSCURA* FROM SAN DIEGO COUNTY, CALIFORNIA, AND EXTREME
NORTHERN BAJA CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	30	115.4-127.0	121.10±0.57	3.13	2.58
		First-year..	32	114.0-123.3	117.41±0.43	2.44	2.08
	F	Adult.....	20	111.3-120.0	116.25±0.60	2.68	2.30
		First-year..	23	110.3-116.9	113.30±0.43	2.08	1.83
Tail	M	Adult.....	30	127.0-145.1	135.57±0.81	4.43	3.27
		First-year..	30	122.3-137.5	129.70±0.67	3.70	2.85
	F	Adult.....	18	120.2-138.0	127.67±0.94	4.00	3.14
		First-year..	22	119.0-131.3	124.36±0.77	3.62	2.91
Bill length	M	Adult.....	31	15.8-20.4	18.30±0.21	1.10	6.47
		First-year..	28	17.0-21.2	18.77±0.16	0.86	4.58
	F	Adult.....	20	15.0-19.4	17.41±0.23	1.01	5.80
		First-year..	19	16.3-19.2	17.64±0.17	0.76	4.32
Bill depth	M	Adult.....	29	7.8-9.4	8.71±0.08	0.42	4.78
		First-year..	27	8.0-9.4	8.63±0.07	0.35	4.02
	F	Adult.....	18	7.7-8.9	8.26±0.07	0.32	3.85
		First-year..	19	7.4-8.6	8.10±0.07	0.28	3.51
Bill width	M	Adult.....	31	7.2-9.5	8.24±0.09	0.51	6.18
		First-year..	28	7.1-9.1	8.33±0.09	0.49	5.91
	F	Adult.....	20	7.2-8.8	7.90±0.08	0.37	4.71
		First-year..	19	7.1-8.8	8.00±0.11	0.47	5.88
Tarsus	M	Adult.....	30	36.6-41.6	38.80±0.19	1.05	2.72
		First-year..	32	36.1-41.1	39.02±0.19	1.00	2.79
	F	Adult.....	20	35.0-39.8	37.77±0.25	1.10	2.92
		First-year..	24	35.9-40.5	37.95±0.22	1.09	2.86
Hind toe	M	Adult.....	31	11.8-14.0	12.70±0.08	0.45	3.52
		First-year..	32	12.0-13.7	12.80±0.08	0.47	3.70
	F	Adult.....	20	11.2-13.5	12.29±0.13	0.58	4.76
		First-year..	24	11.5-13.3	12.26±0.09	0.44	3.62
Middle toe	M	Adult.....	30	17.1-19.8	18.87±0.12	0.67	3.53
		First-year..	32	16.5-20.0	18.69±0.12	0.68	3.64
	F	Adult.....	19	16.8-19.5	18.10±0.15	0.67	3.73
		First-year..	24	17.4-19.2	18.17±0.11	0.54	2.96
Weights (gm.)	M	6	77-82	79.0		
	F	3	69-73	71.8		

Bernardino Mountains represent a resident population, for piñon woodland is known to be present there (A. H. Miller, MS).

In Los Angeles and Orange counties, scrub jays have spread locally and have become established in planted groves of fruit and nut trees in areas where formerly

TABLE 14

MEASUREMENTS OF A. C. OBSCURA FROM LOS ANGELES, SOUTHWESTERN SAN BERNARDINO, ORANGE, AND RIVERSIDE COUNTIES, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	36	117.9-126.6	121.65±0.42	2.54	2.09
		First-year..	33	114.2-123.3	118.82±0.45	2.60	2.19
	F	Adult.....	29	112.8-122.0	117.76±0.43	2.33	1.98
		First-year..	33	107.6-119.6	113.85±0.51	2.94	2.58
Tail	M	Adult.....	36	129.1-144.2	135.94±0.73	4.36	3.21
		First-year..	33	122.4-141.8	130.85±0.84	4.82	3.68
	F	Adult.....	29	120.6-137.5	127.83±0.76	4.11	3.23
		First-year..	33	114.3-131.7	123.18±0.83	4.75	3.85
Bill length	M	Adult.....	38	17.5- 21.3	19.41±0.16	1.02	5.23
		First-year..	27	17.6- 19.9	18.74±0.13	0.67	3.57
	F	Adult.....	26	16.0- 19.1	17.81±0.16	0.82	4.60
		First-year..	24	16.7- 19.4	17.84±0.17	0.82	4.59
Bill depth	M	Adult.....	36	8.1- 9.7	8.99±0.07	0.40	4.44
		First-year..	25	8.1- 9.8	8.77±0.07	0.35	4.00
	F	Adult.....	28	7.7- 8.8	8.26±0.06	0.29	3.54
		First-year..	24	7.8- 8.7	8.23±0.05	0.26	3.21
Bill width	M	Adult.....	38	7.5- 9.3	8.50±0.07	0.42	4.92
		First-year..	27	7.4- 9.1	8.34±0.07	0.38	4.56
	F	Adult.....	29	7.5- 8.8	8.01±0.07	0.40	4.97
		First-year..	24	7.5- 8.4	7.91±0.05	0.26	3.31
Tarsus	M	Adult.....	38	36.7- 41.7	39.39±0.15	0.94	2.39
		First-year..	34	36.5- 41.6	39.36±0.21	1.22	3.10
	F	Adult.....	34	36.2- 40.2	37.97±0.17	0.90	2.37
		First-year..	32	35.0- 40.4	37.86±0.21	1.20	3.17
Hind toe	M	Adult.....	38	11.8- 13.8	12.91±0.07	0.45	3.51
		First-year..	34	11.8- 14.1	12.88±0.10	0.58	4.50
	F	Adult.....	29	11.2- 13.3	12.28±0.09	0.50	4.07
		First-year..	33	11.2- 13.2	11.99±0.08	0.43	3.63
Middle toe	M	Adult.....	38	17.8- 20.3	19.35±0.09	0.56	2.89
		First-year..	34	17.7- 20.8	19.24±0.15	0.88	4.57
	F	Adult.....	29	16.8- 19.8	18.10±0.13	0.69	3.83
		First-year..	32	17.1- 19.7	18.05±0.10	0.55	3.07

the species was absent. Robertson (1931:204) states that at Anaheim jays have been established as residents since at least 1912; subsequent colonization has taken place in orange groves at Buena Park and Cypress. This local spread apparently occurred from east to west (Robertson, *ibid.*). At Azusa, Woods (1932:238) found jays resident in almond orchards; he cited this observation as an example of general extension of the local range of *Aphelocoma* throughout the Los Angeles area.

In the Sierra San Pedro Mártir, scrub jays range altitudinally from 2,100 feet on the Pacific side up to 8,500 feet (Grinnell, 1928:147). In the San Jacinto Mountains they occur up to 6,000 feet (Grinnell and Swarth, 1913:261), and in the San Bernardino Mountains up to 6,800 feet (Grinnell, 1908:84). There are several records of fall vagrants at higher elevations, reaching 7,000 to 7,500 feet and occurring there in atypical habitat (Grinnell, 1908:84; van Rossem and Pierce, 1915:164).

Comparisons.—As *obscura* is smaller and darker than *californica*, it is easily distinguished from *superciliosa*, which is lighter and larger than both. In *obscura*, blue coloration of head and neck is more purplish than in *superciliosa*; the back is more brown (less grayish); under parts show a more dusky wash; under tail coverts are more frequently tinged and darker when tinged. Percentage differences between typical *obscura* (table 12) and *superciliosa* of the San Joaquin Valley (table 19) are as follows: wing, -4.0; tail, -4.2; bill, -4.4; tarsus, -4.6.

Compared with *cactophila* to the south, *obscura* is larger and contrastingly darker throughout; head and neck are a Deep Dull Violaceous Blue rather than grayish blue; the back is darker with less gray; under parts show a more dusky wash; under tail coverts are tinged in 80 per cent of males of *obscura* but in only 15 per cent of *cactophila*. Percentage differences between *obscura* (table 12) and *cactophila* (table 15) are as follows: wing, +2.4; tail, +5.1; tarsus, +2.7.

Geographic variation and intergradation.—Variability in color of the population in the Sierra San Pedro Mártir is relatively limited and is comparable to that of samples analyzed elsewhere, from the Cape region of Baja California (*hypoleuca*) or from the north coast of California (*caurina*). In several specimens from the lower western slopes of the Sierra San Pedro Mártir (near Ensenada and El Alamo), blue areas are less purplish and slightly duller than in typical *obscura* (LMH 3388, MVZ 49930, SD 11092, all adults); in these specimens, color of back and under parts is comparable to typical *obscura*.

Southward, possible intergradation with *cactophila* within the range of *obscura* is suggested by only one specimen, an adult male from Santa Eulalia (AM 93175); in shade of blue on the pileum it is intermediate between *cactophila* and *obscura*; the back is lighter than in typical *obscura*, but not intermediate between those two races; under parts are comparable to lighter variants of *obscura*, although the under tail coverts are strongly tinged.

Northward, intergradation with *californica* occurs over a relatively long distance, from the border of Baja California to the San Bernardino and San Gabriel mountains. Specimens from San Diego County are clearly referable to *obscura*; in size they are comparable to that race (table 18). Greater variability in measurements as well as color of these birds suggests an intergrading population, however. In color the majority of specimens are comparable to typical *obscura*. Color of back, throat, and sides of chest is similar; but in a few specimens, blue areas are less purplish and the smoky wash of the under parts is somewhat reduced. Tingeing of under tail coverts is also reduced in degree, but occurs as frequently as in *obscura*. Specific examples of specimens suggesting intergradation may be cited; an adult male from the Cuyamaca Mountains (SD 11315) is less purplish about the head than typical *obscura*; a first-year male from San Diego (SD 2858) is of a

duller blue (Tyrian Blue—Deep Dull Violaceous Blue on pileum) than typical first-year males, with considerable blue suffusion on the back and lighter under parts; one first-year and one adult female from Witch Creek (CM 142493, 142494, respectively) are lighter than typical representatives of these classes.

The main area of intergradation with *californica* occupies the San Jacinto, Santa Rosa, San Bernardino, and San Gabriel mountains. Variability in color is relatively great, including ranges of *obscura* and *californica*; moreover, there are paler (less purplish) variants that are exceptional. Thus, in the series of adult males, one example is as strongly colored as typical *obscura* (JEL 4584, Summit); another has the dark back of *obscura*, but the less purplish head coloration of *californica* (CM 142468, San Fernando Valley); a third has a light, gray-suffused back, suggesting *superciliosa* of the lower San Joaquin Valley (MVZ 33777, Pasadena); a fourth is of a duller blue than either *obscura* or *californica* (MVZ 3104, Valle Vista). In adult males, under tail coverts are tinged in approximately 60 per cent of the specimens; occasional specimens (for example, CM 142466) are comparable to *obscura* in intensity of tingeing.

In the series of adult males from this area of intergradation which I have examined, specimens approaching *obscura* preponderate; moreover, in size (table 14) these birds are closer to *obscura* than to *californica*. They are therefore referred to the former race. It should be emphasized that in appraising the racial affinities of birds from Los Angeles, Orange, and Riverside counties, careful segregation of age and sex classes must be made; although in sizable series adult males demonstrate closer resemblance to *obscura*, certain individuals may diverge from both *californica* and *obscura*. The same appears to be true of adult females and first-year birds.

A series of nineteen specimens from the Little San Bernardino Mountains is of interest in that general coloration is dark and tends to be more similar to *obscura* in color of under parts than is true to the west and southwest. Thus, intergradation with *californica*, clearly seen among specimens from Los Angeles County, is obscured at various localities to the east, in the Little San Bernardinos. In hue of blue, most of the specimens differ from both *obscura* and *californica* in averaging less purplish than either of these races. The pileum of four adult males varies from Dark Tyrian Blue—Tyrian Blue to Deep Dull Violaceous Blue—Dark Tyrian Blue. In five first-year males the range is the same, but three of them fall at the dark extreme. Four adult females range from Dark Tyrian Blue—Tyrian Blue to Dark Tyrian Blue—Deep Dull Violaceous Blue; these also average less bright than adult males, a difference which cannot be described with the use of Ridgway's terms because of the limited number of standards he provides. Under tail coverts of fourteen of the nineteen specimens (approximately 75 per cent) are tinged with light blue. In color of back, variants resembling both *obscura* and *californica* occur together with others that are duller and grayer than either. In color of under parts, with one or two exceptions, the fresh-plumaged specimens resemble *obscura*. In size these specimens do not differ from *obscura* to the west, in southwestern San Bernardino and Los Angeles counties.

The tendency of the population of the Little San Bernardino Mountains to depart from both *californica* and *obscura* in color of blue areas and back seems to be the

result, in part at least, of genetic interchange with a population of a lighter, duller race (*cana*) to the east, which is separated from the former by a lowland gap of at least twenty miles. But because of continuity in the habitat of scrub jays along the axis of the San Bernardino Mountains, it would be expected that the population in the Little San Bernardinos, at the eastern end of that axis, would be influenced even more from the west. This is what the color characters of the specimens from the Little San Bernardinos show. The possibility remains that the resemblances between them and specimens of *cana* may be the result of selective action of more or less similar environments as much as they may be the result of genetic interchange between the two populations. But in any event the population of the Little San Bernardinos is continuous with the much larger one of the San Bernardino Mountains to the west, and genetic influence of the latter upon the former is probably considerable.

Ecologic distribution.—In the Sierra San Pedro Mártir, woodland within which scrub jays are to be found is dominated by piñons (*Pinus quadrifolia* and others), juniper (*Juniperus californica*), and oaks (*Quercus chrysolepis* and *Q. palmeri*), together with various shrubs (chiefly *Ceanothus* spp., *Sambucus*, *Arctostaphylos* spp., *Adenostoma*, and *Cercocarpus*) (Nelson, 1921:104). At lower elevations along the Pacific coast, woodland and chaparral are characterized by other oaks (*Q. agrifolia* and *Q. dumosa*), buckeye (*Aesculus*), ash (*Fraxinus attenuata*), and various scrubs (*Ephedra*, *Artemisia*, *Eriogonum*) (Nelson, *loc. cit.*). Lamb (1925–1927, MS) has noted scrub jays in oaks and sycamores on the Santo Domingo River, and in thickets of willow and toyon (*Photinia*) in the Valle de la Trinidad. At Concepción and Las Cruces he found them in canyons filled with oaks, willows, and pines, and on adjoining slopes and ridges covered with various chaparral forms, as chamise, manzanita, and *Ceanothus*.

In the region of San Matías Pass, which separates the Sierra San Pedro Mártir from the Sierra Juárez, occurs a vegetation of a more xeric character, composed of mesquite (*Prosopis glandulosa*), barrel cacti (*Echinocactus*), small agaves, and scattered desert scrubs, but also including piñons (Nelson, 1921:pl. 2; Goldman, 1916:314, 334). Scrub jays are known to occur at this locality (SD 17216, taken March 27, 1936); they probably breed also, but this has not been determined definitely. The plant cover of San Matías Pass thus contains several dominant forms of desert vegetation similar to the more vigorous local growths of the same kind of vegetation to the south along the east bases of the Sierra San Pedro Mártir (Nelson, 1921:106). The latter are of an arid and semitropical character, and represent the northern outposts of a flora occupying much of central Baja California where it is inhabited characteristically by scrub jays of another race (*cactophila*). From the available information it appears that *obscura* is similar to more northern races in its ecological association with specific genera of trees and shrubs making up the predominant chaparral and woodland distributed over much of California and northern Baja California. It is not known whether *obscura* inhabits any of the desert vegetation adjoining piñon woodland on the east or south slopes of the Sierra San Pedro Mártir—that is, whether the differences in the habitat relations of *obscura* and *cactophila* are bridged in the behavior of the former. It is probable but not certain that there is a geographic gap in the distribution of

these two races, reinforced by a gap in the specific physical character of their respective habitats. Specimens from the northern margin of the range of *cactophila* which I have examined strongly suggest admixture of characters of *obscura* (see p. 243); but evidence of admixture of characters of *cactophila* along the southern margin of the range of *obscura* is negligible. The situation is thus somewhat perplexing and can be resolved only after a study of local distribution of scrub jays in relation to physical and biotic barriers.

To the north, in the Coast Ranges of southern California, the woodland is generally similar to that of the Sierra San Pedro Mártir. Scrub jays have been recorded in piñons, oaks, junipers, willows, and associated shrubs (Cooper, 1874:17; Sharp, 1907:88; Grinnell, 1908:84; Hanna, 1936:39). In the eastern reaches of the Little San Bernardino Mountains, A. H. Miller (MS) has recorded scrub jays in growths of piñons, scrub oak, junipers, and yuccas.

***Aphelocoma coerulescens cana*, new subspecies**

Type.—Adult male, no. 94204, MVZ; north side of Eagle Mountain, 4,000 feet, Riverside County, California, October 19, 1945; collected by R. C. Stebbins, orig. no. 288.

Racial characters.—Compared to *californica*, lighter and grayer; pileum, hind neck, and sides of neck lighter, duller, and less purplish (Dark Tyrian Blue—Tyrian Blue); back lighter and grayer (Hair Brown—Drab); streaking of throat similar or slightly lighter; lower breast and belly washed with slightly more gray brown; under tail coverts entirely white or tinged terminally with dull grayish blue. In size, according to dimensions of available specimens, similar to populations neighboring *cana* to the west (assigned to *obscura*), thus more or less intermediate between *californica* and typical *obscura* and probably closer to latter; bill distinctly less heavy basally than in *californica*. Measurements of available specimens are given in the table.

	Adult male MVZ 94204, type Oct. 19, 1945	Adult female MVZ 94205 Oct. 20, 1945	Adult female MVZ 93535 May 16, 1945	Adult female SU 2 Oct. 6, 1946
	mm.	mm.	mm.	mm.
Wing.....	123.5	117.7	119.8	116.7
Tail.....	144.2	132.8	125.3	126.3
Bill length....	19.0	16.2	16.6	16.9
Bill depth....	8.5	8.1	8.3	8.0
Bill width....	8.3	8.2	7.5	7.6
Tarsus.....	39.1	37.6	38.7	39.0
Hind toe.....	12.0	12.1	12.4	12.7
Middle toe....	18.3	17.8	18.6	18.4
Weight (gm.)...	77.7	68.7	67.0

Geographic distribution.—Eagle Mountain in eastern Riverside County, California; recorded at elevations of 4,000–4,800 feet; separated from the geographically closest population of *A. coerulescens* by a distance of approximately twenty miles to the west, which includes the lowlands of Cottonwood Pass, the barren Cottonwood Mountains, and the eastern reaches of the Little San Bernardino Mountains in the Joshua Tree National Monument. *A. c. cana* is separated from *A. c. nevadae* in the Providence Mountains by a desert barrier approximately eighty miles wide.

Evidently other populations of pale, dull, small scrub jays occur along the east

slopes of southern California mountains wherever the generally steep terrain and altitude permit the development of scrub woodland or islands of chaparral. That such occurs in extreme northern Baja California, on the east slopes and near the crest of the Sierra Juárez, is indicated by an adult female collected three miles west of Alaska, 3,500 feet, in an area of piñon pine, by I. L. Wiggins and H. O. Hill (SU 3). Color of pileum in this specimen falls between Tyrian Blue and Dark Tyrian Blue; this, together with dull gray back color and light under parts, separates it strikingly from *obscura* of the Sierra San Pedro Mártir and the west slopes of the Sierra Juárez. For the time being, at least, it seems best to place this specimen with those of *cana* from Eagle Mountain and to consider that the present-day distribution of this race is discontinuous. Further evidence bearing upon this view is given on p. 239.

Comparisons.—In the light of the foregoing characterization it is evident that differences between *cana* and the dark-colored and geographically neighboring race *obscura* are greater than those between *cana* and *californica*. Compared with *obscura*, *cana* is strikingly lighter, duller, and less purplish. *Cana* provides a step between *californica* and *obscura* only in the character of light, dull brownish-gray wash over lower breast and belly, which is stronger in *cana* than in typical *californica* of the central California coast. In this one respect, then, *cana* suggests *obscura*.

Compared with *superciliosa* of the San Joaquin Valley, *cana* is smaller; blue areas of the head are duller (more gray) and the back is more gray.

Percentage differences between dimensions of the single available adult male and average dimensions of adult males of *californica*, *obscura*, and *superciliosa* are given in the table. Blanks in the tabulation indicate differences of 1 per cent or less. There is no evidence of significant differences in size between *cana* and *obscura* immediately to the west.

	<i>californica</i> (Central coast, table 4)	<i>obscura</i> (Sierra San Pedro Mártir, table 12)	<i>superciliosa</i> (San Joaquin Valley and foothills, table 10)
Wing.....	...	+ 1.9	— 2.2
Tail.....	— 5.0	+ 6.5	+ 2.1
Bill length.....	+ 4.3
Bill depth.....	— 7.2	...	— 9.3
Bill width.....	— 5.2	...	— 7.5
Tarsus.....	— 3.8	...	— 4.3

Intergradation.—Only three specimens are available from Eagle Mountain, the type and two adult females. These, along with the adult female from extreme northern Baja California, are similar in all characters and stand apart from specimens representing more western populations of both *obscura* and *californica* and intergradient populations between them. The lighter, grayer dorsal coloration of *cana* suggests the interior race *nevadae*, which is present in the Providence Mountains to the north; but *cana* is apparently completely isolated from it. In all characters, *cana* is clearly a differentiate of the *californica* group of races, and its approach toward *nevadae* would seem to me to indicate rather a degree of parallel

selective influence of factors in similar environments. Both races occur in outposts of the piñon-juniper woodland on the periphery of the Mojave Desert.

Specimens from the Little San Bernardino Mountains to the west and northwest of Eagle Mountain are dark and sharply distinct from those of *cana*. (For a discussion of these see p. 235.) This evidence suggests that population interchange between *cana* and *obscura* occurs only sporadically, and at that probably rarely.

The placement of the specimen from Alaska, northern Baja California, with *cana* is supported by a few specimens recently collected along the eastern border of the distributional range of the scrub jay in eastern San Diego County. The limited evidence now suggests that what is observed in jays of Eagle Mountain and of the eastern, upper slopes of the Sierra Juárez probably occurs also in other areas along the eastern side of the southern California mountain ranges which contain suitable habitat and are partly isolated from the widespread populations of scrub jays to the west. The specimens from eastern San Diego County are dull-colored, and approach, but do not reach, the extreme seen in *cana*. It now appears that although a trend toward the differentiation of a pale race may occur in local areas in eastern San Diego County as at points to the north and south, owing to the more or less continuous distribution of scrub jays to the west and to the larger size of their populations, this trend is overcome by genetic interchange between them. The reverse has already been observed; that is, in the population to the west, dull variants suggesting *cana* occur, and population variability is greater than in either *obscura* of the Sierra San Pedro Mártir or *californica* of the central California coast. (See p. 235.)

Ecologic distribution.—On Eagle Mountain, woodland and scrub typically inhabited by *A. coerulescens* are sparse (A. H. Miller, MS). Junipers and piñons are widely scattered; scrub oak and mountain mahogany are present, but are not abundant. The main area of occurrence of the biota which includes the scrub jay is above 4,000 feet. It would appear that the population of scrub jays on Eagle Mountain is a small one. The specimen from extreme northern Baja California was collected in an area of scattered piñons (*Pinus monophylla*).

Aphelocoma coerulescens cactophila

Racial characters.—Compared with *californica*, coloration lighter; blue areas of head less purplish and lighter (Grayish Violaceous Blue—Chapman's Blue, or Chapman's Blue); back lighter (Drab, or Drab—Hair Brown); under parts similar to *californica* except that throat shows less streaking, breast and belly are almost white, and blue of collar is lighter; under tail coverts tinged in 15 per cent of males. In size, smaller than *californica*; percentage differences in adult males are as follows: wing, -3.8; tail, -6.2; bill length, not different; tarsus, -6.6. Wing-tail ratio, 0.919:1. (See also table 15.)

Juvenal plumage.—Upper parts lighter and more grayish (Hair Brown, or Hair Brown—Drab) than those of *californica*; dull blue wash on pileum reduced or lacking; superciliary line variable, similar to *californica*; under parts lighter (less pale brownish gray), necklace pattern generally reduced in mid-region to pale, irregular band; under tail coverts lighter (pallid gray wash); ankle feathers lighter, becoming whitish in some instances.

Geographic distribution.—Central part of the peninsula of Baja California from the lower western slopes of the Sierra de Calamajué (Yubay) south to the Pacific coast at Santa Rosalía Bay; thence southward west of the Vizcaino Desert

TABLE 15
MEASUREMENTS OF *A. C. CACTOPHILA*

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	25	114.0-124.2	118.30±0.51	2.54	2.13
		First-year..	15	112.7-120.6	116.20		
	F	Adult.....	23	110.4-117.6	114.26±0.55	2.61	2.28
		First-year..	14	108.1-116.5	112.36		
Tail	M	Adult.....	25	121.9-136.4	128.80±0.69	3.47	2.70
		First-year..	15	116.6-133.4	126.07		
	F	Adult.....	22	120.6-132.8	124.91±0.64	2.99	2.40
		First-year..	14	116.1-124.0	120.71		
Bill length	M	Adult.....	25	17.5- 21.0	18.80±0.17	0.86	4.57
		First-year..	16	16.8- 20.5	18.81±0.23	0.92	4.89
	F	Adult.....	20	16.0- 19.2	17.52±0.21	0.95	5.42
		First-year..	13	15.9- 20.5	18.17		
Bill depth	M	Adult.....	25	8.4- 10.0	9.20±0.07	0.35	3.84
		First-year..	15	8.2- 9.7	9.00		
	F	Adult.....	20	8.1- 9.5	8.65±0.08	0.34	3.93
		First-year..	13	8.1- 9.1	8.55		
Bill width	M	Adult.....	25	7.9- 9.5	8.64±0.08	0.33	4.40
		First-year..	16	7.4- 9.0	8.42±0.10	0.42	4.97
	F	Adult.....	21	7.3- 9.2	8.22±0.09	0.42	5.11
		First-year..	13	7.1- 9.0	8.29		
Tarsus	M	Adult.....	25	35.5- 40.8	37.94±0.50	1.48	3.90
		First-year..	16	35.2- 40.4	37.98±0.33	1.33	3.50
	F	Adult.....	21	34.2- 39.9	36.27±0.28	1.30	3.58
		First-year..	13	33.6- 39.3	36.09		
Hind toe	M	Adult.....	25	11.8- 14.1	13.14±0.12	0.61	4.64
		First-year..	16	12.0- 13.8	12.95±0.11	0.44	3.40
	F	Adult.....	23	11.7- 13.6	12.43±0.10	0.50	4.02
		First-year..	14	11.3- 13.3	12.22		
Middle toe	M	Adult.....	25	17.4- 20.6	19.40±0.18	0.90	4.64
		First-year..	16	17.8- 20.3	19.26±0.18	0.72	3.74
	F	Adult.....	23	17.0- 20.1	18.58±0.17	0.80	4.31
		First-year..	14	17.0- 20.3	18.64		
Weights (gm.)	M	10	71 - 89	79.5		
	F	7	62 - 80	74.0		

on the Pacific side to Magdalena Bay and on the gulf side to at least Loreto (26° N), but probably farther south along the coast (including Carmen and San José islands?) as well as the plateau and lower slopes along the west side of the Sierra de la Giganta.

North of Yubay and the Sierra de Calamajué, low mountain passes and plains

with scant and stunted desert scrub apparently form a barrier separating *cactophila* from *obscura* (Nelson, 1921:26, 28, 112; Huey, 1942:433). The southward distributional relations of *cactophila* and possible contacts with *hypoleuca* are not known. The southern part of the Magdalena plain separates *hypoleuca* from *cactophila* of the Magdalena Bay area (Nelson, 1921:43), where scrub jays occur typically in mangrove swamps; south of Santa Margarita Island, mangroves apparently do not occur again until Cape San Lucas is reached (*ibid.*:109), and jays are probably absent between Santa Margarita Island, or the neighboring mainland, and Todos Santos. I have seen no specimens from the southern parts of the Sierra de la Giganta, and the desert plain separating that range from the mountains of the Cape region may serve as a partial local barrier at least, although it is but ten miles across at the narrowest point. Along the gulf coast, scrub jays may range southward to La Paz Bay, but no records are available. Evidence of direct intergradation with *hypoleuca* is lacking.

Two specimens from Santana (28°40' N), now in the Museum of Comparative Zoölogy, have been listed under the names *obscura* (Thayer and Bangs, 1907:138; Oberholser, 1918b:481; Grinnell, 1928:146) and *californica* (Swarth, 1918:410). This locality is well within the range of *cactophila*. Santana is placed by Oberholser and Grinnell near lat. 29°20'; it is correctly placed, as above, in Grinnell's gazetteer (1928:30). The specimens in question represent *cactophila*.

Comparisons.—For comparison of *cactophila* and *obscura* see page 234.

Cactophila is separable from *hypoleuca* primarily by smaller size, especially by shorter length of wing and tail. In color, *cactophila* is more variable than *hypoleuca*, blue areas averaging duller and less purplish (approaching or reaching Chapman's Blue on pileum); the back shows less grayish cast and is thus slightly browner; under parts are washed with more smoky tones, but never reach intermediacy between *hypoleuca* and *obscura*; under tail coverts are usually white, as in *hypoleuca*; over the northern third of the range of *cactophila*, including the type locality, darker variants tending toward *obscura* introduce added variation and mixture of color characters. (See p. 243.) Percentage differences between *cactophila* (table 15) and *hypoleuca* (table 16) are as follows: wing, -2.6; tail, -5.3; bill length, -4.8; tarsus, -1.4.

Geographic variation and intergradation.—The race *cactophila* is distinguished from *hypoleuca* primarily by smaller size. The difference is greatest in length of tail. The values of d/σ_d for several measurements, based on comparisons of adult males, are: tail, 5.7; wing, 4.9; bill length, 4.3; tarsus, 2.8. Average weights of adult males of the two races differ by 5.3 gm. (tables 15 and 16); the smaller race *cactophila* averages approximately the same weight as the race *obscura* to the north.

Specimens from the Magdalena Bay region fall into the size range of *cactophila* from the central part of the peninsula and are therefore included in that race. A tendency in size toward *hypoleuca* might be expected at this southerly point, but actually most adults of both sexes fall near or below the average of *cactophila*. As a matter of fact, more specimens of the mangrove-inhabiting jay of Magdalena Bay than are now available may show that the characters attributed to *cactophila* show up as well or better there than along the main axis of the peninsula. There are also slight but suggestive color differences between *hypoleuca* and *cactophila*

of the Magdalena Bay area, not apparent northward near the type locality of *cactophila*, where a color trend toward *obscura* is obvious.

Although my studies confirm the presence of a race additional to the two listed by the A.O.U. Check-list (1931) from Baja California, the degree of difference between *cactophila* and *hypoleuca* proves to be less than that claimed by Huey (1942:434) when first-year birds are segregated from adults. Of nine specimens of *cactophila* listed by Huey which I have examined, seven are first-year birds and two are adults; of the ten specimens of *hypoleuca* listed by him, two are first-year birds, eight are adults. This differential in representation of the two age groups led to exaggerated average differences between the two samples. Thus his differences of 6.2 and 14.2 mm. in wing and tail length, respectively, emerge as only 3.1 and 7.2 mm. when specimens are segregated according to age and when more are measured. (See tables 15 and 16.) Huey (1942:432) also characterized *cactophila* as having a bill smaller than that of *hypoleuca* and with the angular gonyes of that race rather than the "sharper, attenuated shape of more northern forms." Variability in shape of bill, greater in upper Californian races than in *cactophila*, obscures any such difference; the best that can be said is that the attenuated form of bills of scattered individuals among upper Californian races does not appear in *cactophila* or *hypoleuca*; angular gonyes appears fairly frequently, however, among the upper Californian races. Further, the foot and tarsus of *cactophila* were characterized as "lighter-boned." While this is probably true so far as birds from the central portion of the peninsula are smaller than either *hypoleuca* or *obscura*, I do not find such a character "obvious to the eye"; as a matter of fact, when specimens are segregated into sex and age groups and corresponding classes of each race compared, I fail to see any real difference.

Color characters of *cactophila* are more difficult to appraise. Although Huey (1942:432) is correct in stating that in color this race is closest to *hypoleuca*, the situation is more complex than is implied by his statement that "*cactophila* is barely beyond the range of variation shown by a series of *hypoleuca*." Certain color characters represent a step toward *obscura*; in others, *cactophila* resembles *hypoleuca*; in one, shade of blue on pileum, it suggests a step away from either *hypoleuca* or *obscura*.

In the Magdalena Bay region the blue of the head averages duller and less purplish than in *hypoleuca*. Most adult males fall between Grayish Violaceous Blue and Chapman's Blue (SD 15236, for example) or reach the latter color (AM 181651); one adult male (BS 196368) is comparable to the most purplish variants of *hypoleuca*. All specimens show less gray cast on the brown back, but are comparable to *hypoleuca* in color of under parts. White streaking or paling of the forehead, best seen by looking straight at the face, appears in most specimens from Magdalena Bay, but is absent in typical *hypoleuca*; more specimens are needed, however, to attribute any significance to this character.

The presence of whitened foreheads on these specimens recalls the Floridan race *coerulescens*, which is of a duller blue coloration than any of the Pacific coast races. It is of interest that this character occurs best developed among specimens from Baja California (*cactophila* and *hypoleuca*) in the duller-colored birds, namely, the first-year females. A remarkably dull specimen from Magdalena Bay

(SD 15238, probably a female, Light Tyrian Blue on the head) shows a marked paling of the forehead; a second specimen from San José del Cabo (CM 161717), although of a slightly richer blue, shows a similar paling; on both, the collar pattern is lacking on the middle of the breast, and blue on sides of breast is appreciably reduced and then largely replaced with dull grayish brown.

North of Magdalena Bay, a trend toward *obscura* is seen in increasing smokiness of lower breast and darkness of back. This trend, beginning on the Pacific side as far south as San Jorge (SD 18463 and others), is most evident north of the Vizcaino Desert. First-year males collected north of Punta Prieta, near the northern range margin of *cactophila* (SD 13816, 13840) approach *obscura* most closely: in color of lower breast and belly certain individuals fall midway between *obscura* and *hypoleuca* (BS 196362, SD 13840); back coloration may be almost as dark as that of *obscura* (SD 13816, 13840). The remaining first-year birds and adults show under parts washed with more pallid brownish gray and backs darker (Hair Brown) than those to the south.

Near the northern limit of *cactophila*, blue or bluish areas are more variable than other color characters. Under tail coverts are tinged most strongly in certain first-year males: those of two specimens (SD 13816, 13840) are comparable to typical *obscura* (Dutch Blue to Light Windsor Blue). Among females the strongest tingeing of under tail coverts again appears among first-year birds. Or the under tail coverts of first-year birds may be almost white (BS 196362, Yubay, probably a male). Among adults, males as well as females, under tail coverts show slight or no blue tinge. To the south they appear as in typical *hypoleuca* in all age classes. In blue coloration about the head, first-year males again reveal greater variation, ranging from Chapman Blue to almost Deep Dull Violaceous Blue (SD 13816, BS 196365). But true intermediacy between *obscura* and *hypoleuca* is not reached; among adults it is approached only by one February-taken adult male (SD 11782, twenty-five miles north of Punta Prieta), though its color may be misleading because of a moderate amount of wear. Adult males generally average *less purplish* than first-year birds, and even as far north as Yubay (BS 196360) the pileum may appear duller (between Chapman Blue and Tyrian Blue) than that of typical *hypoleuca*. Most specimens from the northern range limits of *cactophila*, chiefly first-year birds of both sexes (SD 13840, BS 196359), but also certain adults (BS 196360), show the throat area more heavily streaked with gray, suggesting the darker throat of *obscura*.

This analysis suggests admixture of characters of *obscura* near the northern limits of *cactophila*, evident chiefly in first-year birds. It is probable that actual interbreeding occurs through the wandering of occasional birds across a distance of sixty to seventy miles of desert separating the Sierra San Pedro Mártir from the Sierra de Calamajué. A first-year female of *obscura* taken in January at San Fernando (MVZ 59581) was probably such a wanderer. If interbreeding occurs, first-year birds would be expected to show mixed characters to a greater degree than the adult population; it does not seem that the mixed characters of birds from the northern margin of *cactophila* can be explained otherwise. Farther south, color characters are less variable, and it would have been preferable, in my opinion, to name *cactophila* from, for instance, the San Bruno area, or possibly the Magdalena

Bay region, rather than from the northern limits of the range (three miles north of Punta Prieta). The duller blue coloration of what I would regard as typical *cactophila* (south of the Vizcaino Desert) is a slight difference and one difficult to detect in limited material, but real nevertheless. Such a difference might be expected on the basis of climate, which is more arid in the mid-regions of the peninsula than in the Cape region. It should be emphasized that fresh-plumaged *adult* males, taken in September, October, and November, best demonstrate this difference.

Ecologic distribution.—Perhaps nowhere over its range does *A. coerulescens* occur in habitats so "atypical" of the species as a whole as in central and southern Baja California. On the opposite Mexican mainland, where a related and fairly comparable arid tropical flora occurs (Johnston, 1924:966; Shreve, 1937:113), *Aphelocoma* is absent and is replaced in part at least by another jay (*Cissilophus*). For an understanding of this seemingly anomalous situation, a brief résumé of the probable history of the biota of Baja California is necessary.

The Cape region of Baja California has been isolated from the Mexican mainland since at least the late Tertiary (Johnston, 1924:969). Before this period a land connection probably was present, and a Sierra Madran biota prevailed. Up to the Pliocene, the Cape region was separated from California proper by a water barrier, and it is possible that the Cape area existed temporarily as an island. In the late Pleistocene the present peninsula came into existence, with the obliteration, probably at the same time, of any connection to the Mexican mainland. A critical change in environment, possibly cooling of the climate accompanied by increased precipitation, led to extinction of most of the species then present. The nature of the faunal and floral relationships of the Cape area to the Mexican mainland remains doubtful, however (Nelson, 1921:103; Johnston, 1924:966). Invasion of the peninsula southward to the Cape by Californian plants and animals then followed. With subsequent changes toward a drier climate, certain species disappeared from mid-regions of the peninsula; others persisted over the length of the peninsula because of greater adaptability, or absence of competition, or both. Of the latter species, *A. coerulescens* is an example.

That the terrestrial vertebrates of Baja California are derived almost entirely from California and adjacent parts of southwestern North America is well known (Nelson, 1921:103; Grinnell, 1928:7). This contrasts with the derivation of the vegetation, which is composed of species representing three different floral elements (Nelson, *op. cit.*): Californian (chiefly chaparral and woodland), Sonoran (desert scrub), and Sinaloan (arid tropical forest). Those Baja Californian birds derived from the Californian avifauna (Grinnell, 1928), including *Aphelocoma*, and characteristic of the woodland and chaparral vegetational types, can be subdivided into three main distributional classes: (1) species which range only into northern Baja California, as *Gymnorhinus cyanocephalus*, *Chamaea fasciata*, *Toxostoma redivivum*, *Dendroica nigrescens*, *Dendrocopos nuttalli*, *Calypte anna*, and so on; (2) species presumably distributed over the entire length of the peninsula at one time, but now occurring only in the mountains of the Cape region and in northern Baja California, as *Empidonax difficilis*, *Vireo huttoni*, *Sitta carolinensis*, *Parus inornatus*, *Pipilo maculatus*, *Aimophila ruficeps*, etc.; (3) species distributed over all or most of the peninsula and thus associated in part with an

environment more xeric than that with which the Californian fauna is identified, as *Lophortyx californica*, *Poliophtila caerulea*, *Amphispiza belli*, *Pipilo fuscus*, *Psaltiriparus minimus*, *Thryomanes bewickii*, *Lanius ludovicianus*, *Myiarchus cinerascens*, *Phalaenoptilus nuttallii*, and *Aphelocoma coerulescens*. The last group includes species (*Amphispiza*, *Lanius*, *Myiarchus*, and *Phalaenoptilus*) which are not restricted to chaparral, woodland, or moister vegetational types, but range into more xeric habitats, usually desert scrub. In general their ecologic range in Baja California presents no unexpected circumstances. But a number of these species here occur almost entirely in habitats which, compared with other parts of their range, are decidedly drier or warmer. *Lophortyx californica*, *Thryomanes bewickii*, and *Aphelocoma coerulescens* are examples. Of the Baja Californian races of *Aphelocoma*, this is true chiefly of *cactophila* occupying the waist of the peninsula.

Cactophila inhabits a desert vegetation regarded as one of the richest and most varied of all known desert floras (Nelson, 1921:106). With the exception of a few local colonies of trees at higher elevations, no true forest or woodland occurs between the Sierra San Pedro Mártir and the Sierra de la Laguna of the Cape region (*ibid.*). Along the middle of the elevated interior plateau just west of the main mountain chain, beginning southeast of San Fernando and continuing southward to opposite Magdalena Bay, is a thick desert vegetation of yuccas, agaves, palo-verdes, ironwoods, mesquites, acacias, and other species of scrub (Nelson, *ibid.*). Various cacti, representing eleven genera, are prominent (Goldman, 1916:351). The scrub jay is a characteristic associate of this vegetation; in the mountains, which for the most part are barren or covered with only scant scrub (Nelson, 1921:62), jays probably occur in the well-vegetated lower canyons of the western slopes. Jays and their nests have been observed or collected in mesquites (*Prosopis* spp.), elephant wood trees (*Veatchia discolor*), and acacias (Bryant, 1889a:24; Lamb, 1927, MS). More interesting, however, is the common occurrence of *Aphelocoma* in the coastal swamps of mangrove (*Rhizophora mangle*) (Bryant, 1889b:293; Anthony, 1925:298). Similar swamps on the coasts of southern Florida and Mexico are not inhabited by this or, so far as known, any other species of jay.

Aphelocoma coerulescens hypoleuca

Racial characters.—Compared to *californica*, blue areas of head lighter (Grayish Violaceous Blue); back lighter (Drab) and suffused generally with more gray, suggesting the race *coerulescens* of Florida; under parts similar to *californica* but throat less streaked, and breast and belly almost white; sides of breast behind blue areas variably washed with pallid brownish gray; under tail coverts usually white but variably tinged with pale blue or gray in approximately 15 per cent of adult males; ankle feathers lighter (Drab Gray), tinged with pallid blue; rectrices and remiges lighter and less purplish (between Deep Orient Blue and Tyrian Blue). In size, slightly smaller than *californica* in all dimensions except length of bill, which is larger; percentage differences in adult males are as follows: wing, -1.3 per cent; tail, -0.9; bill length, +4.9; tarsus, -5.3. Wing-tail ratio, 0.893:1. (See also table 16.)

Juvenal plumage similar to that of *cactophila*.

Geographic distribution.—Cape region of Baja California north and west to La Paz and Todos Santos; probably found also on the island of Espíritu Santo, judging by proximity to mainland and descriptions of environment (Goldman, 1916:357; Nelson, 1921:92).

TABLE 16
MEASUREMENTS OF *A. C. HYPOLEUCA*

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	36	117.4-127.4	121.47±0.39	2.32	1.91
		First-year..	16	114.1-122.9	119.13±0.59	2.37	1.99
	F	Adult.....	29	110.0-119.8	116.72±0.40	2.18	1.87
		First-year..	19	108.9-119.0	114.63±0.61	2.68	2.34
Tail	M	Adult.....	36	127.3-143.2	136.06±0.81	4.87	3.58
		First-year..	16	122.8-138.4	132.12±0.92	3.69	2.79
	F	Adult.....	29	118.4-136.2	129.77±0.75	4.05	3.12
		First-year..	18	112.6-129.6	123.22±1.03	4.38	3.56
Bill length	M	Adult.....	36	17.8- 21.9	19.75±0.15	0.88	4.47
		First-year..	13	18.0- 20.9	19.37		
	F	Adult.....	29	17.7- 20.5	18.86±0.15	0.79	4.23
		First-year..	17	17.4- 20.4	18.61±0.20	0.82	4.42
Bill depth	M	Adult.....	34	8.4- 10.0	9.21±0.06	0.38	4.11
		First-year..	11	8.4- 9.6	9.09		
	F	Adult.....	29	8.2- 9.4	8.69±0.06	0.30	3.44
		First-year..	17	8.1- 9.5	8.76±0.08	0.34	3.94
Bill width	M	Adult.....	35	7.5- 9.5	8.57±0.07	0.41	4.78
		First-year..	13	7.9- 9.5	8.79		
	F	Adult.....	29	7.4- 9.3	8.29±0.09	0.51	6.15
		First-year..	17	7.2- 9.2	8.25±0.13	0.53	6.42
Tarsus	M	Adult.....	35	36.5- 40.2	38.49±0.16	0.97	2.52
		First-year..	16	37.5- 40.6	39.52±0.19	0.77	1.95
	F	Adult.....	29	34.2- 38.9	37.19±0.23	1.23	3.31
		First-year..	19	34.1- 38.9	37.53±0.31	1.31	3.49
Hind toe	M	Adult.....	36	12.6- 14.3	13.42±0.08	0.50	3.72
		First-year..	16	12.9- 14.3	13.64±0.10	0.39	2.86
	F	Adult.....	29	12.1- 14.0	12.92±0.10	0.52	4.03
		First-year..	19	11.8- 13.9	13.02±0.12	0.53	4.07
Middle toe	M	Adult.....	35	17.9- 20.8	19.66±0.11	0.64	3.44
		First-year..	16	18.4- 20.6	19.77±0.16	0.64	3.22
	F	Adult.....	28	17.7- 20.6	18.79±0.13	0.69	3.67
		First-year..	18	18.0- 20.0	19.05±0.14	0.58	3.04
Weights (gm.)	M	10	77 - 95	84.8		
	F	12	68 - 86	76.9		

Nelson (*ibid.*:120) lists *Aphelocoma californica hypoleuca* as characteristic of the "Lower Sonoran" and "Arid Tropical" zones; this is followed by several subsequent authors. Scrub jays range upward into the "Upper Sonoran" zone of the Victoria Mountains, however; the restricted area of this zone does not constitute a basis for minimizing, in any distributional interpretation, the fact that jays are

present there. Brewster (1902:125) speaks of them as being "generally distributed . . . from the seacoast to the tops of the highest mountains." Belding (in Belding and Ridgway, 1883b:348) records them in the Victoria Mountains as "moderately common." A series of specimens from the Sierra de la Laguna have been examined by the writer. Brewster (1902:123) suggests migration of jays from these mountains to lower elevations during winter (dry) months, but this seems doubtful except so far as local movements might lead to temporary desertion of typical habitat.

Comparisons.—For comparison of *hypoleuca* and *cactophila* see page 241.

Variation.—Birds of the Cape region (table 16) display individual variation comparable in degree to that seen in the Monterey district of coastal California. More variation might be expected, since birds range from the arid tropical, sea-coast levels up into the piñon-oak forests of the Sierra de la Laguna; but this is not borne out by material at hand.

Under tail coverts of adult females are tinged only on occasional specimens and then not so strongly as in males. With the exception of retained juvenal feathers, first-year males do not differ significantly from adult males in coloration in the series which I have examined. Blue areas of first-year females are duller than those of adults, reaching a shade in dullest specimens between Deep Orient Blue and Tyrian Blue. Under tail coverts of first-year females are consistently white.

There is no evidence of intergradation between *hypoleuca* and *cactophila* in the series which I have examined; the distributional relations of the two races have been discussed (p. 241).

Ecologic distribution.—In the Cape region, scrub jays range from the mangrove swamps and arid tropical vegetation along the coast up into the woodlands of the Sierra de la Laguna. In no other part of its relatively large area of distribution does *A. coerulescens* occur over so wide a range of environments as in the Cape region. Its altitudinal range extends from sea level to between 5,000 and 6,000 feet.

Below 4,000 feet the vegetation is more or less comparable to that inhabited by *cactophila*, with cacti, mesquites, and acacias predominating (Nelson, 1921:109). Recorded observations report jays in mesquite (*Prosopis juliflora*) and paloverdes (*Cercidium torreyanum* and *Parkinsonia aculeata*), as well as riparian thickets (Bancroft, 1930:33). Many nests are placed in the dense foliage of arrow trees (*Sapium biloculare*) (Bancroft, loc. cit.).

At higher elevations the habitat occupied by *Aphelocoma coerulescens* is more comparable to that of the Sierra San Pedro Mártir, namely, woodlands of oak, piñon, madrone (*Arbutus peninsularis*), and various shrubs, such as *Sambucus*, *Photinia*, *Garrya*, *Ribes*, *Salix*, and *Nolina* (yucca) (Nelson, 1921:104, 105). From the historical standpoint it may be noted that the piñon (*Pinus cembroides*) and associated oaks (*Quercus devia* and *Q. idonea*) occurring in the Victoria Mountains appear similar or more closely related to Mexican species than to those of northern Baja California (Goldman, 1916:314, 321-322); this relationship will remain in doubt, however, until the systematics of both piñons and oaks are better understood. A third species of oak (*Q. brandegei*), growing at lower elevations (500-1,500 feet) along canyons and alluvial valley bottoms (Nelson, 1921:105), is

also said to be more closely related to the Mexican flora. Avian species occurring south of the Sierra San Pedro Mártir only in the woodland and moister habitats of the higher Victoria Mountains, however, are apparently most closely related to the corresponding races on the Sierra San Pedro Mártir.

Apelocoma coerulescens superciliosa

Racial characters.—Characters displayed by specimens from northeastern California and the San Joaquin Valley are here regarded as typical of *superciliosa*. Differs from *californica* in being paler; pileum, hind neck, and sides of neck and chest less purplish (Deep Cadet Blue) and, in northeastern California, grayer (approaching Dark Tyrian Blue or Tyrian Blue); back suffused with more gray or blue gray, thus lighter than in *californica*; under parts lighter (with less smoky wash); collar and sides of chest less purplish; under tail coverts usually white (tinged lightly with pallid gray or blue gray in only 15 per cent of adult males). In size, larger than *californica*; comparisons of adult males are given in the table. Blanks in the tabulation indicate differences of one per cent or less. (For other measurements and sex, age, and intraracial differences in size, refer to tables 17–22.)

	San Joaquin Valley (table 19)	Northeastern California (table 22)
	<i>per cent</i>	<i>per cent</i>
Wing.....	+ 2.7	+ 4.2
Tail.....	+ 2.9	+ 2.3
Bill length.....	+ 5.5	...
Tarsus.....	...	— 1.5
Wing-tail ratio.....	0.894:1	0.913:1

Juvenal plumage: lighter and grayer than that of *californica*; crown, pileum, sides of head, and chest Hair Brown; back Drab; collar Drab to Light Drab; under parts with less smoky wash, lower breast largely, belly and sides entirely, white; crown area suffused with paler blue.

Geographic distribution.—San Joaquin and Sacramento valleys from Mount Pinos north to southern central Oregon (Eagle Point, Jackson County; Summer Lake and Hart Mountain, Lake County); westward along the inner foothills of the Coast Ranges (Beegum, Tehama County; Fouts Springs, Colusa County; Mount Diablo, Contra Costa County; Orestimba Peak, Stanislaus County; thence unrecorded south to ten miles northwest of McKittrick, Kern County); absent (?) in the western parts of Merced, Fresno, and Kings counties; east to the foothills and western slopes of the Sierra Nevada and continuing around the northern end of that range eastward and southward over extreme northwestern and western Nevada (Virginia Mountains) south to Alpine County, California (three miles east of Woodfords), and Douglas County, Nevada (Gardnerville); again continuing around southern end of the Sierra Nevada along the west side of the Owens Valley northward to western-central Inyo County (Kearsarge Pass, west of Independence).

In the southern San Joaquin Valley, resident scrub jays are restricted for the most part to local willow growths bordering the main river channels, lakes, or sloughs. They have been recorded in summer at the confluence of the Merced and San Joaquin rivers (Dixon, 1924:52) and at Tulare and Buena Vista lakes (Goldman, 1908:204). E. L. Sumner, Jr. (1930, MS), observed three individuals

TABLE 17

MEASUREMENTS OF A. C. SUPERCILIOSA FROM SACRAMENTO VALLEY AND ADJOINING FOOTHILLS, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	42	117.6-133.3	124.38±0.53	3.41	2.74
		First-year..	25	119.4-131.2	124.80±0.63	3.16	2.53
	F	Adult.....	46	112.6-127.6	120.11±0.54	3.68	3.07
		First-year..	21	111.6-126.8	118.24±0.81	3.73	3.15
Tail	M	Adult.....	41	127.6-152.0	137.56±0.70	4.49	3.27
		First-year..	25	126.8-144.4	134.84±0.83	4.17	3.09
	F	Adult.....	44	121.2-141.3	129.80±0.73	4.88	3.76
		First-year..	19	118.2-135.8	127.00±1.00	4.35	3.43
Bill length	M	Adult.....	42	16.7- 21.7	19.17±0.18	1.17	6.10
		First-year..	23	16.6- 20.5	18.83±0.19	0.93	4.94
	F	Adult.....	43	16.1- 20.3	18.06±0.16	1.03	5.68
		First-year..	20	16.0- 19.2	17.68±0.18	0.82	4.64
Bill depth	M	Adult.....	43	8.5- 10.1	9.26±0.05	0.35	3.78
		First-year..	23	8.8- 10.0	9.22±0.07	0.33	3.53
	F	Adult.....	44	8.2- 9.7	8.85±0.06	0.41	4.61
		First-year..	19	7.9- 9.6	8.77±0.10	0.44	5.00
Bill width	M	Adult.....	43	7.8- 9.5	8.80±0.06	0.38	4.34
		First-year..	23	8.2- 9.4	8.74±0.06	0.31	3.50
	F	Adult.....	45	7.5- 9.4	8.39±0.07	0.45	5.34
		First-year..	20	7.4- 8.8	8.24±0.08	0.38	4.59
Tarsus	M	Adult.....	43	37.6- 42.5	40.30±0.19	1.24	3.09
		First-year..	27	38.3- 42.2	40.30±0.20	1.02	2.37
	F	Adult.....	46	36.0- 41.6	38.81±0.17	1.17	3.02
		First-year..	22	36.0- 41.2	39.09±0.27	1.29	3.30
Hind toe	M	Adult.....	43	12.2- 14.8	13.47±0.08	0.55	4.08
		First-year..	27	12.2- 14.4	13.48±0.09	0.49	3.60
	F	Adult.....	46	11.3- 13.9	12.80±0.08	0.55	4.31
		First-year..	22	11.8- 13.8	12.85±0.11	0.51	3.97
Middle toe	M	Adult.....	42	18.3- 21.5	19.86±0.12	0.77	3.88
		First-year..	27	18.1- 22.3	19.92±0.17	0.89	4.48
	F	Adult.....	45	17.8- 20.5	19.11±0.10	0.65	3.40
		First-year..	21	18.2- 20.4	19.14±0.16	0.73	3.81
Weights (gm.)	M	16	87 -105	96.6		
	F	11	74 - 90	82.7		

in October on the Los Banos Game Refuge, Merced County, which were probably fall stragglers from resident populations to the east. Absence of suitable habitat is an important, if not the chief, factor accounting for the restricted range of scrub jays in the lower San Joaquin Valley, for they breed along the lower slopes of the

Sierra Nevada and in the floor of the valley wherever extensive willow thickets and associated riparian vegetation occur. To the west of the San Joaquin river bottoms and on to the east slopes of the inner southern Coast Ranges, scrub jays have not been collected between Orestimba Peak in Stanislaus County and ten

TABLE 18

MEASUREMENTS OF MALES OF *A. C. SUPERCILIOSA* FROM SAN ANDREAS, CALAVERAS COUNTY, CALIFORNIA, APRIL 26, 1936

	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	Adult.....	39	118.4-131.7	123.90±0.48	3.00	2.42
	First-year.....	23	115.5-130.0	120.83±0.77	3.70	3.06
Tail	Adult.....	38	129.4-148.5	137.21±0.68	4.20	3.06
	First-year.....	23	123.3-140.7	131.83±1.04	4.98	3.78
Bill length	Adult.....	38	17.5- 20.6	18.86±0.13	0.79	4.17
	First-year.....	23	17.3- 21.2	19.12±0.21	1.03	5.35
Bill depth	Adult.....	39	8.5- 10.0	9.26±0.06	0.36	3.87
	First-year.....	23	8.6- 9.6	9.07±0.06	0.27	2.99
Bill width	Adult.....	39	7.7- 9.5	8.64±0.07	0.41	4.70
	First-year.....	23	8.0- 9.7	8.63±0.08	0.39	4.47
Tarsus	Adult.....	38	38.0- 42.5	40.18±0.17	1.04	2.59
	First-year.....	23	38.9- 42.3	40.01±0.19	0.90	2.24
Hind toe	Adult.....	39	12.0- 14.5	13.18±0.09	0.55	4.20
	First-year.....	23	12.3- 14.1	13.24±0.10	0.48	3.60
Middle toe	Adult.....	36	17.4- 21.0	19.50±0.12	0.74	3.80
	First-year.....	21	18.9- 20.8	19.80±0.12	0.57	2.87
Weights M (gm.)	Adult.....	39	84 -108	93.4		
	First-year.....	23	83 -105	90.7		
	Mixed.....	167	71 -104	90.8		
	F Adult.....	11	81 - 98	88.5		
	First-year.....	5	74 - 87	81.9		
	Mixed.....	116	67 - 97	81.7		

miles northwest of McKittrick in Kern County; the region in question is dry and barren.

In Washoe County, Nevada, the known range of *A. c. superciliosa* apparently closely neighbors that of the Great Basin race of the "*woodhousei*" group, *nevadae* (Pitelka, 1945a). Marginal areas where either race or mixed populations occur are the Granite Range, the Pine Nut Range, and possibly the Nightingale Mountains. *A. c. superciliosa* is known from the Virginia Mountains, just west of the latter range. To the east, *nevadae* occurs on the West Humboldt Mountains, Pershing County; it is probably found also on the Stillwater Range, Churchill County,

TABLE 19
MEASUREMENTS OF A. C. SUPERCILIOSA FROM SAN JOAQUIN VALLEY AND ADJOINING
MOUNTAINS, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	34	121.0-132.7	126.26±0.47	2.74	2.16
		First-year..	22	119.3-129.4	123.59±0.54	2.54	2.05
	F	Adult.....	37	112.8-126.8	121.14±0.44	2.66	2.20
		First-year..	22	111.0-123.0	117.86±0.65	3.07	2.61
Tail	M	Adult.....	33	133.6-150.2	141.24±0.67	3.84	2.72
		First-year..	22	127.3-144.0	136.23±1.00	4.75	3.49
	F	Adult.....	34	121.8-142.2	134.76±0.75	4.38	3.26
		First-year..	22	114.6-136.4	129.05±1.00	4.70	3.64
Bill length	M	Adult.....	34	18.2- 22.5	19.85±0.16	0.95	4.80
		First-year..	13	17.6- 21.3	19.60		
	F	Adult.....	36	16.0- 21.6	18.66±0.20	1.18	6.32
		First-year..	12	16.4- 19.1	17.68		
Bill depth	M	Adult.....	34	8.8- 10.3	9.37±0.06	0.33	3.52
		First-year..	13	8.6- 9.5	9.11		
	F	Adult.....	36	8.2- 9.5	8.85±0.06	0.37	4.23
		First-year..	12	7.9- 8.9	8.42		
Bill width	M	Adult.....	34	8.0- 9.8	8.97±0.07	0.41	4.55
		First-year..	13	8.0- 9.5	8.74		
	F	Adult.....	36	8.0- 9.6	8.51±0.07	0.41	4.84
		First-year..	13	7.4- 8.8	8.13		
Tarsus	M	Adult.....	37	38.0- 42.5	40.85±0.17	1.06	2.61
		First-year..	22	37.5- 43.3	40.47±0.26	1.21	2.98
	F	Adult.....	38	36.7- 42.0	39.63±0.18	1.13	2.84
		First-year..	22	35.3- 41.8	39.07±0.34	1.53	4.04
Hind toe	M	Adult.....	34	12.7- 14.4	13.54±0.08	0.44	3.28
		First-year..	22	12.2- 14.7	13.37±0.12	0.54	4.06
	F	Adult.....	37	12.5- 13.9	13.09±0.07	0.40	3.03
		First-year..	22	11.7- 13.5	12.60±0.11	0.52	4.16
Middle toe	M	Adult.....	34	18.2- 21.6	19.98±0.13	0.74	3.69
		First-year..	22	17.9- 21.2	19.56±0.17	0.80	4.11
	F	Adult.....	37	17.9- 20.1	19.32±0.09	0.52	2.70
		First-year..	22	17.2- 20.1	18.69±0.15	0.70	3.77
Weights (gm.)	M	27	86 -108	97.3		
	F	34	74 - 98	84.8		

for specimens of *nevadae* have been collected near Fallon in the fall. On the Pine Forest Range of northern Humboldt County, suitable habitat occurs, but the species has not been reported from there. To the south, *nevadae* has been collected in Mineral and Mono counties, on either side of the Nevada-California line, respec-

tively. The two tongues of the range of *superciliosa* on the east side of the Sierra Nevada thus do not approach each other at all closely.

The relationships of *nevadae* and *superciliosa* between the Pine Grove area in northwestern Mineral County, where the former has been recorded, and Gardner-

TABLE 20
MEASUREMENTS OF A. C. SUPERCILIOSA FROM EAST SLOPES OF SIERRA NEVADA,
INYO COUNTY, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	13	123.7-130.7	127.69±0.59	2.13	1.67
		First-year..	7	118.4-129.1	124.00		
	F	Adult.....	18	118.1-123.2	122.94±0.53	2.25	1.83
Tail	M	Adult.....	13	132.3-151.4	143.00±1.54	5.55	3.89
		First-year..	7	131.8-143.2	136.29		
	F	Adult.....	18	130.9-142.0	135.39±0.69	2.95	2.17
Bill length	M	Adult.....	13	19.0- 21.3	20.19±0.19	0.67	3.32
		First-year..	6	19.1- 22.0	20.25		
	F	Adult.....	17	18.0- 21.5	19.39±0.20	0.84	4.35
Bill depth	M	Adult.....	13	8.3- 9.8	9.20±0.12	0.44	4.76
		First-year..	7	8.5- 9.5	8.91		
	F	Adult.....	18	7.9- 9.3	8.61±0.09	0.39	4.49
Bill width	M	Adult.....	13	8.1- 8.8	8.48±0.07	0.26	3.05
		First-year..	7	7.9- 8.9	8.39		
	F	Adult.....	18	7.3- 8.8	8.12±0.09	0.39	4.78
Tarsus	M	Adult.....	13	38.1- 42.7	40.08±0.36	1.31	3.27
		First-year..	7	38.5- 42.1	40.49		
	F	Adult.....	17	37.5- 40.9	39.04±0.24	0.98	2.50
Hind toe	M	Adult.....	13	12.4- 13.8	13.17±0.11	0.41	3.12
		First-year..	7	12.7- 14.0	13.27		
	F	Adult.....	17	11.9- 13.0	12.50±0.09	0.36	2.85
Middle toe	M	Adult.....	13	18.5- 20.0	19.22±0.17	0.61	3.15
		First-year..	7	18.7- 21.0	19.67		
	F	Adult.....	17	17.6- 19.9	18.53±0.16	0.65	3.50
Weights (gm.)	M	15	76 - 98	87.6		
	F	19	72 - 89	80.0		

ville in Douglas County, where *superciliosa* has been recorded, have yet to be clarified fully. Brief field investigations in late June, 1946, and in October, 1947, confirmed evidence from botanical literature that the piñon-juniper woodland inhabited by scrub jays is distributed continuously along the east slope of the Sierra Nevada and along the Virginia and Pine Nut ranges southward to and over the Sweetwater Range. Scrub jays occur throughout this region, and thus *superciliosa* and *nevadae* meet. Intergradation in this region is discussed on page 262.

Two reports of "*Aphelocoma californica*," as distinguished from "*Aphelocoma woodhouseii*," from the Mono Lake area are probably misidentifications of the latter. These are W. K. Fisher's report from Mono Lake (1902:11) and Stephen's report (*vide* A. K. Fisher, 1893:70) from the "head of the Owens River" (= Long Valley, east of Mount Lyell). Reports of "*woodhouseii*" near Spooner in the Lake

TABLE 21

MEASUREMENTS OF *A. C. SUPERCILIOSA* FROM SOUTH-CENTRAL OREGON (JACKSON AND KLAMATH COUNTIES) AND NORTH-CENTRAL CALIFORNIA (SISKIYOU AND SHASTA COUNTIES)

	Sex	Age group	No. of specimens	Range	Mean
Wing	M	Adult.....	10	123.0-130.6	127.60
		First-year.....	9	119.5-129.5	125.78
Tail	M	Adult.....	10	134.5-144.2	139.60
		First-year.....	9	129.7-143.4	137.22
Bill length	M	Adult.....	8	17.2- 21.6	18.92
		First-year.....	5	17.7- 19.2	18.64
Bill depth	M	Adult.....	8	9.1- 10.5	9.70
		First-year.....	4	9.0- 9.6	9.35
Bill width	M	Adult.....	8	8.3- 9.5	9.00
		First-year.....	5	8.5- 9.0	8.81
Tarsus	M	Adult.....	10	38.8- 42.8	41.39
		First-year.....	9	39.8- 43.3	40.93
Hind toe	M	Adult.....	8	13.1- 14.5	13.77
		First-year.....	9	12.9- 14.4	13.70
Middle toe	M	Adult.....	7	19.2- 21.7	20.29
		First-year.....	9	18.9- 21.2	20.43

Tahoe region and in southeastern Lassen County (Ray, 1901:117; 1910:89) probably refer, in turn, to *superciliosa*. Most of the foregoing records from Nevada have been summarized by Linsdale (1936:84).

In the southern Sierra Nevada, *superciliosa* remains separated from *nevadae* by the Owens Valley. It has not been recorded north of Independence and Kearsarge Pass. The actual northern limits are not far north of these points. Field observations which I made in the area in 1942 revealed that the steep eastern faces of the Sierra Nevada are more or less uninterrupted for a distance of ten to fifteen miles south of Big Pine; a piñon zone, constituting the chief breeding habitat of scrub jays in this region, is absent along these steep slopes. A scrub vegetation dominated by sagebrush (*Artemisia tridentata*) covers parts of these slopes between slide areas up to higher elevations where yellow pine (*Pinus ponderosa*) and other conifers appear. In the vicinity of Big Pine, local colonies of piñons are present in pockets formed by the lower foothills west of Big Pine, but no scrub jays were

TABLE 22

MEASUREMENTS OF *A. C. SUPERCILIOSA* FROM LAKE COUNTY, OREGON, AND EAST SLOPES OF SIERRA NEVADA FROM ALPINE COUNTY NORTHWARD, CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	38	123.0-135.0	128.18±0.44	2.69	2.10
		First-year..	33	120.2-132.4	127.00±0.50	2.88	2.27
	F	Adult.....	17	119.8-127.1	122.65±0.55	2.25	1.84
		First-year..	14	117.3-128.0	123.14		
Tail	M	Adult.....	32	133.5-152.0	140.47±0.89	5.02	3.57
		First-year..	33	127.5-144.0	135.97±0.73	4.20	3.08
	F	Adult.....	13	126.7-137.9	132.92		
		First-year..	14	125.4-137.0	130.86		
Bill length	M	Adult.....	39	16.7- 21.7	18.65±0.17	1.04	5.57
		First-year..	16	17.0- 19.8	18.76±0.18	0.71	3.78
	F	Adult.....	18	15.8- 18.9	17.58±0.20	0.87	4.95
		First-year..	9	15.4- 19.3	16.90		
Bill depth	M	Adult.....	39	8.0- 10.0	9.12±0.07	0.42	4.61
		First-year..	15	8.1- 9.3	8.81		
	F	Adult.....	18	8.0- 9.1	8.56±0.08	0.35	4.06
		First-year..	9	8.1- 8.7	8.41		
Bill width	M	Adult.....	41	7.6- 9.5	8.54±0.07	0.44	5.20
		First-year..	14	7.3- 9.1	8.41		
	F	Adult.....	18	7.7- 9.2	8.23±0.09	0.36	4.42
		First-year..	9	7.3- 8.5	7.96		
Tarsus	M	Adult.....	41	38.3- 42.5	40.03±0.13	0.86	2.14
		First-year..	15	37.8- 41.6	40.36		
		Juvenal....	18	37.5- 42.5	40.02±0.32	1.37	3.42
	F	Adult.....	18	36.4- 40.2	38.55±0.24	1.04	2.69
		First-year..	14	36.8- 40.5	38.92		
Hind toe	M	Adult.....	41	12.0- 14.3	13.29±0.09	0.57	4.31
		First-year..	16	12.3- 14.4	13.44±0.15	0.58	4.33
		Juvenal....	18	12.9- 14.1	13.38±0.07	0.31	2.31
	F	Adult.....	18	12.0- 13.6	12.83±0.10	0.40	3.16
		First-year..	14	12.6- 14.1	13.21		
Middle toe	M	Adult.....	37	18.8- 21.1	19.71±0.10	0.59	3.05
		First-year..	16	18.5- 20.9	19.84±0.14	0.56	2.84
		Juvenal....	18	18.4- 20.3	19.42±0.14	0.58	3.05
	F	Adult.....	18	18.0- 19.5	18.88±0.10	0.44	2.32
		First-year..	14	17.6- 20.1	19.09		
Weights (gm.)	M	27	81 -103	93.8		
	F	10	61 - 94	77.3		

found. Thus the Owens Valley together with steep, nonwooded eastern slopes of the Sierra Nevada form a local barrier between the breeding ranges of *superciliosa* and *nevadae*. As will be discussed beyond, *nevadae* crosses this barrier, at least sporadically, but the main breeding ranges remain discontinuous.

Altitudinal range.—In the Sierra Nevada, scrub jays generally do not range upward beyond the lower margins of the yellow-pine zone, in general from 2,000 to 3,000 feet. Occasional pairs or small populations may occur at higher elevations, but their spotty distribution is apparently related to the local occurrence of suitable scrub habitat on warmer exposures. Available records of upper extremes of occurrence in the breeding season are as follows: 6,000 feet on Mount Pinos (Grinnell, 1904:385), 8,000 feet in the Monache Meadows of Tulare County (Fisher, 1893:70), 5,000 feet in the Yosemite region (Mowbray, 1940:79), 6,000 feet in Placer County (MVZ 24225), 5,700 feet in the Lassen Peak region (Grinnell, Dixon, and Linsdale, 1930:296), 3,600 feet in the Mount Shasta region (MVZ 67850), and 4,300 feet near Klamath Falls, Oregon (AW 190). On the east side of the southern Sierra Nevada the race *superciliosa* ranges from 5,200 to 7,500 feet (west of Olancho and Independence), but probably higher on the warmer east- and south-facing slopes where suitable breeding habitat occurs. In the Lake Tahoe region, scrub jays apparently breed locally up to Bijou at 6,300 feet (Ray, 1918:71; SU 7531, taken June 5, 1911; CAS 58151, taken May 29, 1921) and near Spooner at 6,500 feet (Ray, 1910:89).

After the breeding season there is sporadic wandering upward of single individuals or groups, most of which are probably juvenal or first-year birds. Grinnell (1905:385) observed several individuals at 8,500 feet on the southeast side of Mount Pinos in July. A series of records of vagrants is available from the Yosemite Valley from July to November (Grinnell and Storer, 1924:387; Michael and Michael, 1921:35; C. W. Michael, 1925:111). Full-grown juveniles have been collected early in August at 7,000 and 6,400 feet on the eastern slopes of the Sierra Nevada in Nevada and Sierra counties, respectively (MVZ 17106, 17107). Other fall records from higher elevations are available from Summit, Placer County (6,900 feet), and Lake Tahoe (Belding, 1890:110), and Manzanita Lake (6,000 feet) in the Lassen Peak area (Vogt, 1941:162).

Certain observations from the eastern slopes of the Sierra Nevada suggest the possibility of altitudinal migration in *Aphelocoma*. On a climatic basis this might be expected, since the winters are probably more severe there and in northwestern California and south-central Oregon than in other parts of the range of the "*californica*" group of races. Ridgway (1875:37) states that in the Carson City region, where he spent the winter of 1867-68, scrub jays arrived on April 29; Henshaw (1877:1310) speaks of their leaving the same area by November. In Modoc County, Mailliard (1927:310) observed "a scraggly band of 25 apparently in migration through cottonwoods along Eagle Creek." These statements are only suggestive, however; more data are needed on the local distribution of scrub jays along the California-Nevada line and on differences in local movements of first-year birds versus adult birds.

Comparisons.—For comparisons of *superciliosa* with *oocleptica* see page 221; with *immanis*, page 268.

Superciliosa is larger than any race of the "*californica*" group except *immanis*. In color *superciliosa* approaches the lighter-colored races of Baja California fairly closely; specimens from western Nevada and northeastern California are, for the most part, comparable to *cactophila*; compared with *hypoleuca*, typical *superciliosa* remains slightly darker throughout and less purplish.

Geographic variation and intergradation.—The inclusive race *immanis* of Swarth (1918:415) and the A.O.U. Check-list (1931:223) represents a complex of racial characters and variational trends, an analysis of which provides a basis for an understanding of the interrelations of the entire "*californica*" group of races. Scrub jays of the Sacramento Valley and adjoining foothills are especially variable in characters of color and size of wing and tail; they are, in general terms, the most variable of the Pacific coast races. In several adjoining areas are populations possessing characters which represent, or at least may be regarded as, segregates of the more variable characters observed in the Sacramento Valley. Certain of these segregates are well marked and constitute recognizable races, as *oocleptica* and *californica*; a third such race, *immanis*, *sensu stricto* (Grinnell, 1901:188), is proposed here. The remaining aggregate occupying the Sacramento and San Joaquin valleys and the eastern slopes of the Sierra Nevada in Inyo County, and again from central Nevada north to south-central Oregon, is here treated as one race, *superciliosa*; but as will be seen from the ensuing discussion, the biological interpretation of populations in these areas does not permit any clear-cut nomenclatural designation.

Specimens from the Sacramento Valley show, first, a range of color variation which, although it is not greater than that of any coastal race, includes more individuals that approach either extreme; that is, were quantitative values of color available, their statistical distribution would be platykurtic. Qualitative appraisals of the type made when plumage colors are studied are especially difficult when there is evidence of exceptional variability; but in the series available to me the foregoing interpretation seems to be warranted. Given isolated specimens from this series, I would estimate that 15 to 20 per cent of them could not be separated from *californica* or *oocleptica* on the basis of color or, as will be discussed later, size. With an additional 15 to 20 per cent, separations would be doubtful. The remainder, however, showing less purple on the head and chest and more gray on the back, are distinguishable from specimens representing coastal populations. Color of head, pileum, and sides of neck and chest, in adult males, varies from Deep Cadet Blue—Chapman's Blue (CAS 25634) to Deep Cadet Blue—Deep Dull Violaceous Blue (CAS 28713, MVZ 51795). Of these, approximately 60 per cent fall within the darker half of the color range, 40 per cent within the lighter half. In first-year males the same color range is displayed, but specimens of the lighter type of coloration preponderate. As might be expected, the darkest-colored specimens of both age classes come from the northern part of the Sacramento Valley (Tehama County: MVZ 51795, 45708). In the dullest first-year male (MVZ 53405, Grass Valley), head coloration reaches Tyrian Blue and is comparable to that seen in specimens from northeastern California. Southward, in the San Joaquin Valley, and around the southern end of the Sierra Nevada into western Inyo County, approximately the same color range prevails, but the majority of specimens are of

the light type. Darker variants similar to those of the Sacramento Valley and to coastal specimens are of regular occurrence, however; these have been collected in localities generally near the upper limits of the breeding range of scrub jays on the Sierra Nevada (MVZ 25055, 25057, from the Yosemite region; MVZ 40550, 63784 from northeastern Kern County, 3,900–4,250 feet). Consistently light-colored birds, representing the light extreme of blue coloration at the southern end of the range of *superciliosa*, are obtained along the lower, eastern margin of the San Joaquin Valley (Minkler, Dunlap, Snelling; see list of specimens). In males, shade of blue falls between Deep Cadet Blue and Chapman Blue, reaching the latter in occasional variants (MVZ 82436); in adult females, shade of blue falls between Tyrian Blue—Chapman's Blue and Tyrian Blue—Deep Cadet Blue. In first-year females, blue areas become still lighter and duller (Light Tyrian Blue, MVZ 27239, 27242).

Around the northern end of the Sierra Nevada from the Sacramento Valley and into northeastern California and adjoining parts of Oregon and Nevada, again, blue areas become lighter, but here become grayer, also. Among adult males the head and chest coloration may reach Dark Tyrian Blue—Deep Cadet Blue (SGJ 6553, Summer Lake) or an even more extreme shade, Dark Tyrian Blue—Tyrian Blue (MVZ 94406, Peavine Mountain). Only four fresh-plumaged adult males are available from this area (including two mentioned above); considered alone, these could not be used for any satisfactory evaluation of color variation. In eight additional fresh-plumaged first-year males, however, blue areas remain consistently grayer (Dark Tyrian Blue—Tyrian Blue, as in MVZ 46046, to Tyrian Blue, as in MVZ 43335) than almost all specimens of corresponding age and sex from the Sacramento Valley, and all those from the Willamette Valley.

In south-central Oregon the observed color range remains comparable to that of specimens from the Sacramento Valley. Specimens from Jackson County are similar to dark variants from the latter region; those from Klamath and Lake counties are more mixed, including grayish-blue variants. One adult specimen from Klamath Falls (BS 155533), unsexed, but almost certainly a male (wing, 129.7 mm.; collar area strongly colored), is comparable to lighter variants of *superciliosa* in shade of blue. Northward, however, the more purplish, less grayish color of certain variants from the Sacramento Valley becomes characteristic. In the Willamette Valley, blue coloration may be similar to that of the darkest variants of *californica* or *oocleptica* in certain individuals (SGJ 5081, and AGP no. 1, adult male, Scio, October 10, 1923). But in series, specimens average slightly less purplish on head and chest than those two races and are closest to Grayish Violaceous Blue; under parts, wings, and tail are similar in color to *californica*.

Similar relationships among all these populations of *immanis*, *sensu* Swarth, are seen when the character of back color is analyzed. Variably suffused with gray in the Sacramento Valley, the back becomes most strongly and consistently gray in the San Joaquin Valley and on the eastern slopes of the Sierra Nevada (northeastern California and western Inyo County). This trend toward graying of the back appears strongest among specimens from northeastern California, which show consistently more gray suffusion than specimens from the Sacramento and Willamette valleys. In south-central Oregon the back remains suffused with gray

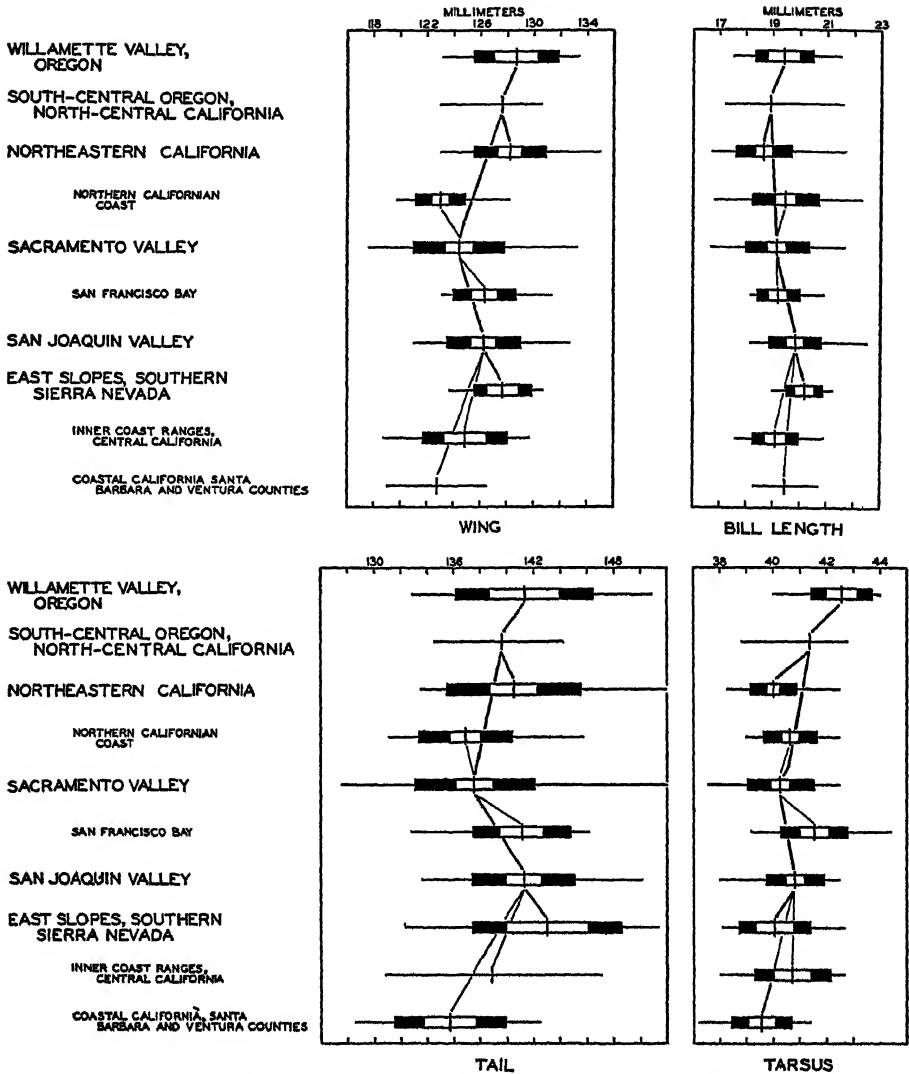


Fig. 7. Individual and geographic variation in *Aphelocoma coerulescens immansis* (Willamette Valley; see fig. 4) and *A. c. superciliosa* (remaining areas indicated in large letters, arranged in north-to-south order). Thick lines connecting averages denote geographic contact. Populations of coastal races neighboring *superciliosa* listed in small letters; geographic contact shown by thin lines. Data represent adult males.

to a variable degree, as seen in the Sacramento Valley. Northward, in the Willamette Valley, back color becomes brownest and comparable to *californica* in certain instances, but averaging slightly grayer.

This analysis of color characters indicates that of three segregates from the array presented by the Sacramento Valley population, one displays darkening of color and the other two display lightening and graying. The latter trend reaches

its extreme development in northeastern California, the former in the Willamette Valley; on the basis of color, specimens from these two portions of the range of *immanis*, *sensu* Swarth, are easily distinguished.

Variation evident in the plumage of adult and first-year birds is also seen in that of juveniles. Those from the Sacramento Valley and adjoining foothills are variable in color, ranging from individuals approaching the extreme of paleness in *superciliosa* (MVZ 48503, central southern Tehama County) to darker variants approaching coastal specimens (MVZ 22746, Glenn County). To the north, pale variants appear as far as Sisson, Siskiyou County (CM 142459, 142460). In south-central Oregon, juveniles approach *californica* closely, but remain slightly grayer (CM 70593, 70594, Eagle Point). In the San Joaquin Valley, pale juveniles predominate at the southern end of the Sierra Nevada (BS 139600, MVZ 20057, 20069), but again, dark variants (BS 139601) occur apparently to the same extent as among adults. Although juvenal plumages of these jays are more variable than adult plumages in any given population, the characteristics of the series representing the Sacramento and San Joaquin valleys are not to be explained alone by individual variation, and the close correspondence in behavior of characters between adults and juveniles further supports the foregoing interpretation. Still further correspondence is seen in the juvenal plumages of specimens from northeastern California, where color reaches an extreme of paleness and grayness (MVZ 14380, 14383, 14390), the back becoming Light Drab—Light Grayish Olive.

Among the several populations here considered, characters of size parallel or exceed those of color in complexity of geographic relations. The general behavior of these characters is best seen in a diagram (fig. 7) in which one main series of five samples is arranged in north-to-south order, from the Willamette Valley to the San Joaquin Valley and thence to the eastern slopes of the southern Sierra Nevada. This series is interrupted by three samples representing areas neighboring the north-south axis (northeastern California, *caurina*, and *oocleptica*). At the lower end of the series are added two samples of *californica* (central-inner and southern), both adjoining populations of the San Joaquin Valley to the west and south. Thus there are represented all areas inhabited by the race *immanis*, *sensu* Swarth, as well as all adjoining areas inhabited by some other race of the "*californica*" group.

Turning first to the wing and tail, we find lengths more or less correlated in pattern of variation among the several samples. The Sacramento Valley population is the most variable; the range of variation for this sample exceeds the lower extreme and almost exceeds the upper extreme observed in other samples. Measurements given in table 17 show that this variability obtains in all sex and age classes; evidence that this does not represent a geographically heterogeneous sample is provided by an excellent restricted sample of sixty-two adult and first-year males, all collected in late April, 1936, in the vicinity of San Andreas, Calaveras County (table 18). Variability in lengths of wing and tail in this single population, as in the sample representing the Sacramento Valley, is seen to be greater than that of any other sample of *superciliosa*.

According to the diagram (fig. 7), wing and tail become longer northward, eastward, and southward along the Sierra Nevada, but shorter coastally, except in the race *oocleptica*, in which these parts are as large as, or larger than, in the San

Joaquin Valley. The wing becomes longest in the Willamette Valley; among remaining interior samples it becomes longest on the east side of the Sierra Nevada. The tail is of approximately equal size in samples from the Willamette and San Joaquin valleys, but becomes longest on the east side of the southern Sierra Nevada. Coastally, while *oocleptica* shows increase in length of tail, the increase is relatively less than that in wing length and body mass. (See tables 8 and 9.)

It should be noted that averages for measurements of wing and tail in the Sacramento Valley are smaller than those of central-interior *californica*. Indeed, averages from the San Andreas population (table 18) are comparable to or even smaller than those from the Sacramento Valley; the differences are slight but appear consistently in almost all measurements. The sample from San Andreas leaves little doubt about the occurrence of jays of small size in the Sierra Nevada foothills; no additional samples comparable to that from San Andreas are available. Smaller specimens in the sample representing the Sacramento Valley and adjoining foothills come from scattered localities in Tehama, Glenn, Sutter, Placer, and Yolo counties; thus, again, the smaller size of these birds represents not just a local tendency but a greater regional variability.

In length of tarsus the larger size of jays from the Willamette Valley is even more striking than in wing or tail. Southward, the feet become large again only in *oocleptica*; among interior samples they become smallest on the east side of the Sierra Nevada.

The pattern of variation in bill size is seen only partially in a comparison of bill lengths among the several samples. While the bill of *immanis* in the Willamette Valley is of only intermediate length when compared with other races, it is deeper and broader than the bill of any other race of the "*californica*" group (table 23). The extreme heaviness of the bill of *immanis* is augmented by a greater convexity of the gonys, such as appears in races of central and southern Baja California. Comparing the remaining samples, perhaps the most striking point to be observed is the fact that the shortest and longest bills both occur on the east side of the Sierra Nevada. The short bills of scrub jays inhabiting northeastern California represent an extreme reached or exceeded only by the southern Californian race *obscura*. In this character, jays of northeastern California contrast strikingly with those of the Sacramento and San Joaquin valleys and of the Great Basin as well. Some correlated contrast in foot habits probably exists; data on the extent to which scrub jays of northeastern California and south-central Oregon feed in juniper foliage, for instance, are desirable.

Southward, in the central valley, a gradient toward increased length of bill reaches its maximum on the east side of the southern Sierra Nevada. Here the length of bill is intermediate between that of jays of the San Joaquin Valley and that of the Great Basin.

Specimens from south-central Oregon east of the Cascade Range display evidence of intergradation toward *immanis*. In color they are similar, in the main, to dark variants from the Sacramento Valley, and thus are suggestive of *immanis*. On the basis of color, certain specimens (as SGJ 4412, Summer Lake) are difficult to separate from *immanis*; but representatives of the two races are separable when sizes of bill and feet are considered. Such dark color variants have been examined

from as far south as Susanville, Lassen County, California (MVZ 88162). Only occasional specimens from southeastern Oregon (as SGJ 3492, Adel) suggest the duller, grayer coloration of scrub jays to the south in western Nevada and adjoining parts of California. In all these areas, however, scrub jays are similar in the important characters of size.

On the basis of this analysis of the geographic pattern of variation in the inclusive race *immanis* of Swarth, comment may now be made on the nomenclatural disposal of jays occupying the range ascribed to that race. It has been shown that *immanis*, or *superciliosa* (A.O.U. Committee, 1945:445), includes populations occupying several peripheral geographic areas which differ more or less from each other, and which may be regarded as segregates of the variable populations occupying the Sacramento Valley and adjoining foothills. Three of these segregates have been combined heretofore under the name *immanis* or *superciliosa*; the first occupies the Willamette Valley of Oregon; the second, northeastern California and adjoining parts of Oregon and Nevada; and the third, the San Joaquin Valley. Among these three segregates, the strongest differences are seen between the first and the second. The second and third are fairly similar in that they display similar trends in the several racial characters considered here.

In this entire complex, the two extremes to be recognized are placed rather eccentrically from a geographic point of view: the first, in the Willamette Valley, is easily set aside under the name *immanis*, based on specimens taken at Scio, Oregon (Grinnell, 1901); the second, in northeastern California, clearly distinguishable from *immanis*, is separable under the name *superciliosa*. But included under this name are all populations occupying the San Joaquin and Sacramento valleys (whence the name was first applied), north-central California, and south-central Oregon. Differences between specimens from the San Joaquin Valley and northeastern California are too slight to be recognized nomenclaturally; only in bill size is there a noteworthy difference, but an adequate separation of specimens from the two regions cannot be made in series available to me.

Relationships of the races superciliosa and nevadae.—To the east of *superciliosa* occurs another race of *A. coerulescens*, representing, however, the "*woodhousei*" group of races, so strongly differentiated from the "*californica*" group that the two were for many years accorded specific rank, most recently in 1918 by Swarth. Facts now available strongly suggest that between these two groups of races there is partial isolation. Where their representatives, *superciliosa* and *nevadae*, meet, they intergrade over only a surprisingly restricted area, as in west-central Nevada (see fig. 4), or they hybridize sporadically, as in southeastern California, on the west side of the Owens Valley. The two races also meet in northwestern Nevada, but there is no evidence at present that they interbreed there. These several situations may now be discussed in detail.

In northwestern Nevada, several areas of extensive, more or less barren lowland seem to form local barriers which would appear to separate populations of *superciliosa* and *nevadae*. These are the deserts of central Washoe, northeastern Pershing, and western Humboldt counties, Granite Spring Valley of Pershing County, and the Carson Sink in Churchill County. Only two records of *nevadae* to the west of this diffuse lowland barrier are known to me, and in both instances the speci-

mens are first-year individuals. One was taken in November at Sutcliffe (GW 1460); as *superciliosa* breeds a short distance to the west, in the Virginia Mountains, it is likely that individuals of the two races come into contact here at least occasionally in fall and winter. The second record is that of a specimen (BS 139709) taken in May on the east side of the Granite Range along Granite Creek. That *nevadae* may meet *superciliosa* in the Granite Range is indicated by a specimen of the latter race, a first-year female, obtained there on the lower eastern slopes of Granite Peak by the writer in October, 1947. However, if scrub jays actually breed in the Granite Range, the population is small: no extensive areas of suitable habitat occur there, and in the area studied only two or three individuals were seen. Because all the specimens available from the critical areas enumerated above are first-year birds, they may be regarded as merely drifters occurring in local islands of marginal habitat but nowhere associated with a self-maintaining population. The possibility that *superciliosa* and *nevadae* may interbreed in northwestern Nevada cannot be denied, but it appears to me now that if such interbreeding occurs, it is rare.

In northeastern California, more than anywhere else in the range of the "*californica*" group of races, certain similarities between that group and the "*woodhouseii*" group may be seen. At first sight these similarities might be considered to indicate genetic interchange between the two groups, but in my opinion another explanation better serves the facts. The similarities are as follows: longer wing in proportion to body size and tail length, reduced body size, shortened tarsus, smaller (narrower and shallower) bill, and paling and graying of plumage. Actually, in color of under parts and pattern of throat markings, *superciliosa* retains characteristics typical of the "*californica*" group; also, the dusky wash over the under parts is reduced so that populations of northeastern California come to have the whitest under parts of any race of *coerulescens* in the United States, thus contrasting strongly with the neighboring race *nevadae*. Moreover, the lighter, grayer plumage of *superciliosa* does not indicate necessarily immediate genetic relationship with *nevadae*; the plumage of *superciliosa* remains a more intense, less grayish blue than is shown by *nevadae* of the Great Basin. Finally, *superciliosa* of northeastern California differs from *nevadae* in bill length; the bill of *superciliosa* is shorter here than that of jays of any neighboring geographic areas. In this character also, then, *superciliosa* of northeastern California contrasts strongly with *nevadae*. The similarities that do occur may best be regarded as influences of parallel selective factors in similar environments.

Evidence of intergradation has been obtained only from a restricted area in west-central Nevada, from the southern part of the Virginia Range south to the southern end of the Pine Nut Range and the mountains connecting the latter range with the Sierra Nevada. Over this restricted area there is no significant break in the piñon-juniper zone inhabited by scrub jays. *Superciliosa* and *nevadae* meet there, and intergradation between them is abrupt. Specimens obtained to the east of the upper Truckee Valley, on the lower west slope of the Virginia Range, represent intergrades, but they fall closer to *superciliosa*. Specimens from the Pine Nut Range, Douglas County, represent *nevadae* in most characters; but the whitish color of the belly and under tail coverts suggests *superciliosa*. At present there is no evidence of intergradation on the east slope of the Sierra Nevada south to

Alpine County, California, where the previously reported occurrence of *superciliosa* was confirmed by my field studies. On the other hand, typical *nevadae* has been collected in extreme western Mineral County, Nevada, not far southeast of the Pine Nut Range. Thus crossbreeding between these strikingly different races, representing, respectively, coastal and interior groups of races, occurs along the Virginia-Pine Nut range axis over a distance of no more than fifty miles. It seems improbable that this could occur were not the two forms partially isolated reproductively.

On the eastern slopes of the southern Sierra Nevada there is evidence of hybridization between *superciliosa* and *nevadae*; at best this apparently occurs sporadically, even though the distance across the Owens Valley which separates the two races is relatively short, and descent into the valley during the winter on the part of both races would seem to facilitate crossbreeding. (See p. 253.) In late May and June, 1942, a field party from the Museum of Vertebrate Zoölogy obtained a total of forty-three specimens on the west side of the valley from Olancha to Independence. Among these, together with eight additional specimens from other sources, only two (4 per cent) are clearly of the race *nevadae*. Six others (12 per cent) show hybrid characters; they may be offspring of parents which represent the two races or which themselves are hybrids of various degrees, removed one or more generations from an initial cross between individuals of the two races.

One specimen of *nevadae* is an adult female (MVZ 84947), taken west of Lone Pine at 6,600 feet on May 26, 1942. It was observed feeding young out of the nest, and examination of the collected specimen revealed a well-developed brood patch. When compared with adult females of *superciliosa* from neighboring localities (for example, MVZ 22504) showing equivalent wear of plumage, the distinguishing characters of this specimen are at once obvious: lighter blue coloration of upper parts, best seen on unworn plumage on side of head and neck and on the wings; strongly tinged under tail coverts; more restricted white throat area, with gray streaking; sharp, long, narrow bill. A second specimen, a first-year male in fresh fall plumage (MVZ 20077), taken at 8,500 feet, south of Carroll Creek, is in all respects an individual of the race *nevadae*; it probably represents a fall wanderer, taken well above, but nevertheless geographically close to, the normal breeding habitat of *superciliosa*.

Among specimens possessing certain characters of *nevadae* are two adult females (MVZ 84936, 84970) taken west of Olancha and Independence, respectively. The first has the pale-blue coloration of *nevadae* together with a darkened throat and breast approaching that race; the under tail coverts are tinged comparatively strongly, although not so intensely as in *nevadae*. Because of the degree of wear it is not possible to appraise the color characters of this specimen accurately; but it may represent a first-generation hybrid. The second adult female has only the pale-blue coloration of *nevadae*; in pattern of markings and color of under parts it is entirely comparable to *superciliosa*. Other females (for example, MVZ 84932) are pale, but these are first-year birds, similar in color to specimens of the same sex and age from the San Joaquin Valley.

One fresh-plumaged adult male (MVZ 20068), taken along Carroll Creek at 5,500 feet, suggests *nevadae* in that blue areas, while retaining a purplishness en-

tirely absent in *nevadae*, are pale (Grayish Violaceous Blue); moreover, the back is heavily suffused with blue gray. In all other respects, especially size and color of under parts, this specimen is comparable to *superciliosa* (Swarth, 1918:417). A second adult male (MVZ 84952), taken west of Independence, may represent another first-generation hybrid, as suggested by pale coloration, darkening of throat and breast, and tingeing of under tail coverts; but again the specimen is too worn to warrant any statement other than that it shows certain tendencies toward *nevadae*.

The two remaining specimens showing characters of *nevadae* are fledglings (MVZ 84946, 84950), both taken west of Lone Pine at 6,600 feet. These differ from six other fledglings taken along the west side of the Owens Valley in that the former are gray on throat, breast, and belly, whereas the latter are white or whitish, except for the collar. The two darker individuals are apparently hybrids, as they are more or less intermediate between juveniles of *superciliosa* and *nevadae* in color of under parts. In both groups, collar markings are of approximately the same color; thus the chief distinguishing feature is one of absence or presence of contrast in color of under parts. The lighter throat area of the hybrids appears somewhat narrower, again suggesting the race *nevadae*. No differences have been detected in the shade of blue among these and additional fledglings from the Great Basin. In color of upper parts, all eight juveniles from the west side of the Owens Valley differ from those of all other Californian areas in being grayer (Hair Brown—Mouse Gray); they differ contrastingly from juveniles of the southern San Joaquin Valley as well as those of northeastern California in being darker. One of the hybrids proves to be the grayest individual (MVZ 84950, dorsum Mouse Gray).

Since under tail coverts contrast strongly in color between the two races, and since these feathers may escape wear fairly well, they provide another basis for comparison. Data on tingeing of under tail coverts among thirty-eight adult or first-year birds of *superciliosa* from the west side of the Owens Valley, excluding the two specimens of *nevadae*, are given in the table. It is at once evident that tingeing occurs in adult males more frequently than in the central valley proper, where approximately 15 per cent of adult males have tinged under tail coverts. In neither shade of color nor degree of tingeing but only in frequency of tingeing does this character suggest introgressive effects from the race *nevadae*.

From this examination of color characters it is evident that crossbreeding of the two neighboring races occurs only sporadically, and may continue apparently through successive generations resulting in varying admixture of the characters of *nevadae*. There is no clear-cut evidence of primary intergradation in the sense of a gradual transition from one race to another (Mayr, 1942:99), or even of full fertility. Data on size suggest intergradation in almost all measurements, which are more or less intermediate between *superciliosa* of the San Joaquin Valley and *nevadae* of the California-Nevada line. There can be no doubt that the intergrading nature of these size characters is, in part at least, affected by crossbreeding with *nevadae*, and perhaps this is the chief factor. Even though crossbreeding may be sporadic, its continuance over successive years may lead to substantial interchange of genes. But there are probably additional factors of selection stemming from certain parallelisms in the environment of the two races on either side of the Owens

Valley, as character of habitat, food, and climate, which lead to similarities. The contrast in color characters remains sharp. The relationships of *superciliosa* and *nevadae* in the Owens Valley appear to illustrate a zone of secondary intergradation: two races, once separated, again adjoin and crossbreed; here the interchange of genetic materials is relatively slight, or at least slow.

Ecologic distribution.—On the foothills and mountain slopes surrounding the Sacramento and San Joaquin valleys, scrub jays inhabit chiefly woodland, chaparral, and stream-border thickets. As elsewhere, preference is shown for areas of varied vegetation, but extensive chaparral areas of monotonous character are also inhabited. The blue oak, Digger pine, and live-oak woodland associations form one of the chief communities with which *Aphelocoma* is associated in the peripheral

Age group	Degree of tingeing		
	Strong (dull blue)	Moderate (pale blue and/or gray)	Absent (white)
MALES			
Adult.....	..	7	5
First-year.....	..	4	1
	..	—	—
Total.....	..	11	6
FEMALES			
Adult.....	1	7	9
First-year.....	0	2	2
	—	—	—
Total.....	1	9	11

parts of the central valley of California. In Tehama County, in June, 1943, scrub jays were observed by the writer in such woodland interspersed abundantly with manzanita (*Arctostaphylos manzanita*) as an interspace and understory shrub and adjoining slopes covered with *Adenostoma* over which jays ranged (pl. 27*b*). Grinnell and Storer (1924:387) found them in similar habitat in the Yosemite region; they report nests in blue oaks and willows (*ibid.*:390). In Madera County, Grinnell (1911:109) found the species nesting in oaks and *Ceanothus* shrubs. Woodland and chaparral habitats of comparable character are described by Grinnell, Dixon, and Linsdale (1930:296) from the western parts of the Lassen Peak region; and to the north, jays are reported from juniper woodland and oak-pine forest edge in Shasta County (Merriam, 1899:119) and oak and chaparral areas in south-central Oregon (Gabrielson, 1931:116). Bendire (1895:374) observed scrub jays near Fort Klamath on hillsides covered with mountain mahogany (*Cercocarpus ledifolius*). In northeastern California and south-central Oregon, jays occur chiefly in an *Artemisia-Juniperus* association typical of that region (Miller, 1937, MS) and in local willow thickets (Grinnell, 1918:190; Marshall, 1937, MS); near Adel a nest was found in an *Artemisia* bush (Miller, *op. cit.*). In the Sacramento and San Joaquin valleys, orchards and streamside communities

dominated by willows form the chief habitats of scrub jays (Tyler, 1913:66, and others). On Mount Pinos, scrub jays occur chiefly in the piñon belt (Grinnell, 1905:385). Occasionally they may occur in the lower parts of the yellow-pine zone, as in the southern Sierra Nevada (R. Hunt, 1920, MS).

On the eastern slopes of the Sierra Nevada, in Inyo County, where local distribution of scrub jays was studied by the writer in late May and June, 1942, woodland of oak (*Quercus chrysolepis*) and piñon (*Pinus cembroides*) formed the chief habitat occupied by this species. In oak-filled draws of the lower slopes and along the lower border of the oak-piñon zone, where the latter interdigitated with a scrub community dominated by *Artemisia tridentata*, *Chrysothamnus nauseosus*, and *Lupinus excubitus*, scrub jays were especially prominent. Northward, west of Lone Pine, woodland areas are composed of fewer species of dominants: piñons interspersed with sagebrush and occasional individual shrubs of *Purshia glandulosa* and *Chrysothamnus*. Here piñons formed the main retreat of scrub jays. Along higher slopes, *Cercocarpus ledifolius* is added as a dominant to the piñon woodland. A *Pinus-Cercocarpus* woodland was also found west of Independence, but here appeared more restricted. There is progressive reduction in the extent of the woodland zone northward from the Olancha area as the slopes of the Sierra become more steep and more monotonous physiographically. Along Little Pine Creek, at 6,000 feet west of Independence, in a stream-border island of relatively rich vegetation, dominated by black oak (*Q. kelloggii*) and yellow pine (*Pinus ponderosa*) with thickets of willow (*Salix lutea*), water birch (*Betula fontinalis*), and cottonwood (*Populus fremontii*), the oaks and associated thickets together with border shrubs of a more xeric character (*Artemisia* and *Ceanothus greggii*) were inhabited by jays. Judging by the presence of recently fledged young, nests of several pairs in this area were placed in dense willow thickets. To the south, along Pinyon Creek, jays were observed ranging from the piñon and mountain mahogany woodland down into cottonwoods and willows along the stream. To the north, along Oak Creek, sclerophyllous oaks (*Q. wislizenii* and *Q. morehus*) were again found, here in association with black oaks and border thickets of willow, birch, and cottonwood. Three pairs of jays were found without difficulty over a relatively short distance along the stream; the species appear as common here as in the foothills west of Olancha. North of this locality, jays of the race *superciliosa* were not found again. As described earlier, the woodland typically inhabited by scrub jays becomes absent or reduced to small local groves for a distance of ten to fifteen miles between Independence and Big Pine.

Apelocoma coerulescens immanis

Racial characters.—Compared with *californica*, slightly lighter in coloration; pileum, hind neck, and sides of neck and chest less purplish (Deep Cadet Blue—Grayish Violaceous Blue); back Hair Brown, suffused only slightly with gray; under parts washed with pale smoky gray, as in *californica*; under tail coverts tinged with pale blue or gray in approximately 60 per cent of males. In size, larger than *californica*; percentage differences in adult males are as follows: wing, +4.6; tail, +2.9; bill length, +3.0; tarsus, +4.8. Wing-tail ratio, 0.911:1. (See also table 23.)

No juvenal specimens of *immanis* have been seen, but on the basis of juvenal characters observed in south-central Oregon (see p. 259) and deductions from the characters of the adult plumages, the juvenal plumage of this race is probably closely similar to, if not indistinguishable from, that of *californica*.

Geographic distribution.—Inner western Oregon between the Coast Ranges and the Cascade Mountains, chiefly the Willamette Valley, from extreme southern Washington (Ridgefield, Clark County) south probably to Douglas County.

Scrub jays do not occur along the Oregon coast and east of the Cascade Range (except in south-central and southwestern Oregon, where the races *superciliosa*

TABLE 23
MEASUREMENTS OF A. C. IMMANTS OF WILLAMETTE VALLEY, OREGON

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	15	123.2-133.4	128.67±0.81	3.16	2.46
		First-year..	12	120.7-128.9	124.83		
	F	Adult.....	9	120.6-129.2	124.33		
Tail	M	Adult.....	15	132.9-150.9	141.27±1.32	5.13	3.63
		First-year..	12	128.6-146.0	137.25		
	F	Adult.....	9	128.5-145.4	135.22		
Bill length	M	Adult.....	13	17.5- 21.5	19.39±0.30	1.08	5.55
		First-year..	11	17.0- 19.9	18.65		
	F	Adult.....	8	17.4- 19.9	18.62		
Bill depth	M	Adult.....	13	9.2- 10.3	9.79±0.07	0.27	2.72
		First-year..	9	9.3- 10.3	9.45		
	F	Adult.....	8	9.1- 9.7	9.25		
Bill width	M	Adult.....	14	8.3- 9.9	9.19±0.11	0.40	4.35
		First-year..	11	7.8- 9.6	8.92		
	F	Adult.....	8	8.1- 9.8	8.85		
Tarsus	M	Adult.....	15	40.0- 44.0	42.56±0.29	1.13	2.65
		First-year..	12	39.2- 44.3	41.73		
	F	Adult.....	9	39.7- 43.0	41.27		
Hind toe	M	Adult.....	14	13.5- 14.9	13.98±0.12	0.43	3.09
		First-year..	11	12.6- 14.7	13.84		
	F	Adult.....	9	13.0- 14.2	13.53		
Middle toe	M	Adult.....	11	20.1- 21.5	20.80±0.15	0.50	2.40
		First-year..	11	19.2- 21.8	20.45		
	F	Adult.....	9	19.1- 20.9	20.03		

and *caurina* are found). The species has been recorded as a fall vagrant, however, southeast of Tillamook, Tillamook County (Walker, 1926:182; also AW 10094, taken October 9, 1937), and on the Columbia River at The Dalles, Wasco County (Henshaw, 1879:307). Following Nuttall's (1840:245) early records of scrub jays ("*Garrulus ultramarinus*") at Fort Vancouver, the first adequate report of the species in Washington was that of Lawrence (1892), who observed it along the Columbia River, again near Vancouver. According to Jewett and Gabrielson (1929:28), scrub jays are not abundant north of Salem and Dallas except on

Sauvie Island in the Columbia River, where a small population is present. Anthony (1886:167) states that they were common in the western part of Washington County in comparison with the area about Beaverton, but locality records west of Forest Grove are lacking.

Comparisons.—*Immanis* differs from *superciliosa* in having a heavier bill, larger feet, and darker (less grayish) coloration. Compared with populations of north-eastern California (table 22), the Sacramento Valley (table 17), and the San Joaquin Valley (table 19), differences between average measurements of these and *immanis*, expressed as percentage of the latter, are given in the table. Variational trends in scrub jays of interior California and Oregon, including *immanis*, have been discussed (pp. 256–261).

	Northeastern California	Sacramento Valley	San Joaquin Valley
Wing.....	...	— 3.3	— 1.9
Tail.....	...	— 2.6	...
Bill length.....	— 3.8	— 1.1	+ 2.4
Bill depth.....	— 6.9	— 5.4	— 4.3
Bill width.....	— 7.1	— 4.2	— 2.4
Tarsus.....	— 5.9	— 5.3	— 4.0

Immanis approaches the coastal races, *caurina*, *californica*, and *oocleptica*, in color more closely than any interior race of the "*californica*" group; but it differs from any of these in being grayer dorsally and less purplish. In these differences *immanis* suggests *superciliosa* of the Sacramento Valley, through variational trends to which reference has been made. Differences between *immanis* and coastal races of California are especially strong when comparisons are made with specimens of *caurina* from the north coast of California and southwestern Oregon, where blue areas of head and chest become most purplish. Specimens from the latter region are appreciably smaller (wing, — 4.4 per cent) and easily separable from *immanis*. In size, *immanis* is similar to *oocleptica*, but averages slightly larger in all measurements. Disregarding geographic placement and presence of other races in intervening areas, differences of size and color might be regarded as inadequate for the nomenclatural separation of *immanis* and *oocleptica*; but characters of color and size of bill are clearly, though weakly, different in the two races.

In size, *immanis* is noteworthy as the largest of the races of scrub jays occurring on the North American mainland. Races of the interior "*woodhousei*" and Mexican "*sumichrasti*" groups all possess longer wings and tails, but only the races of the "*sumichrasti*" group are comparable to *immanis* in size of bill or feet. *Immanis* possesses the stoutest bill of all mainland races. The largest variants among adult males of *immanis* are, in general terms, similar in size to the smallest variants of the large Santa Cruz Island scrub jay, *insularis* (see p. 271); ranges of variation of the two races do not overlap in measurements of wing, tail, bill length, or tarsus; negligible overlap occurs in those of bill depth and middle and hind toes; but in width of bill the overlap is appreciable, the bill of *immanis* being, on the basis of average measurements, only 1.4 per cent narrower than that of *insularis*.

There seems to be no basis for the claim of Grinnell (1901:188) that the tail of *immanis* is proportionally longer than that of *californica*. The wing-tail ratio of adult males of *immanis* proves to be 0.911:1, whereas values of *californica*, *oocleptica*, and *superciliosa* of the Sacramento Valley are 0.896:1, 0.899:1, and 0.907:1, respectively. The vernacular name "long-tailed jay" applied to *immanis*, *sensu* Swarth (1918), is thus a misnomer.

Variation and intergradation.—Adult males, though averaging a lighter shade of blue on head, neck, and chest than *californica*, are almost as purplish as the latter race. All evaluations of color here refer to the dorsum and sides of the head unless otherwise stated. Certain individuals (SGJ 5081) reach Deep Dull Violaceous Blue characteristic of *californica*; the majority, however, fall between Deep Dull Violaceous Blue—Deep Cadet Blue (MMP 363) and Deep Cadet Blue—Grayish Violaceous Blue (MVZ 33788, a co-type). First-year males are chiefly Grayish Violaceous Blue (C 17135) or Grayish Violaceous Blue—Deep Cadet Blue (SGJ 7096); one first-year male (MMP 199) of an exceptional shade of blue is best described as Chapman's Blue—Tyrian Blue. Among adult females, blue areas are Grayish Violaceous Blue or Grayish Violaceous Blue—Chapman's Blue (MVZ 33787, 33790, respectively, both co-types). First-year females reach Grayish Violaceous Blue—Tyrian Blue (C 17132). The back of *immanis* appears slightly lighter than that of *californica* or *oocleptica* (see p. 257); but in certain individuals back coloration becomes comparable to that of the coastal races (SGJ 7097).

Variation in size with relation to adjoining races has been discussed under the race *superciliosa* (p. 259). Intergradation with *superciliosa* to the south probably occurs over a broad belt from the southern end of the Willamette Valley in Lane County southward over Douglas and northern Jackson counties. No specimens have been examined from any part of this area, however. To the west of this belt of intergradation the neighboring race *caurina* reaches its northern limits.

Ecologic distribution.—Few data are available on the habitat relations of *immanis*. The chief vegetational types inhabited are mixed thickets bordering fields and openings and willow thickets along the margins of sloughs and streams (Lawrence, 1892; Bendire, 1895:374; Jewett and Gabrielson, 1929:28). Scrub jays also occur commonly in mixed vegetation of shrubs, as of manzanita and wild plum, and deciduous trees, chiefly oaks (Jewett and Gabrielson, *ibid.*; Gabrielson and Jewett, 1940:422). The vegetation occupied by this species is here, in general, of a marginal character surrounding or interspersed with the main coniferous forest mass. The clearing of forests by man has probably aided in increasing the areas of habitat suitable for this species.

Aphelocoma coerulescens insularis

Racial characters.—Compared with *californica*, much darker; pileum, hind neck, and sides of neck of deeper blue, approaching Cyanine Blue; blue of sides of head, throat, and breast comparably darker; auricular region black; back darker (Clove Brown); under parts similar, except that Light Mouse Gray of lower breast persists over belly; under tail coverts consistently colored and contrastingly darker (Deep Dutch Blue to Slate Blue); ankle feathers darker (Mouse Gray to Hair Brown), the distalmost feathers tinged pale blue (Dutch Blue); upper tail coverts Deep Dull Violaceous Blue; rectrices and remiges darker (Indigo Blue to Dusky Blue). In size, much larger than *californica*; percentage differences in adult males are as follows: wing, +13.8 per cent; tail, +14.5; bill length, +24.9; tarsus, +13.4. Wing-tail ratio, 0.885:1. (See table 24 for

TABLE 24
MEASUREMENTS OF *A. C. INSULARIS*

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	45	134.2-144.4	139.22±0.31	2.06	1.48
		First-year..	28	129.7-137.1	134.36±0.35	1.88	1.40
	F	Adult.....	39	130.2-138.1	132.54±0.30	1.90	1.43
		First-year..	17	126.1-134.0	129.47±0.45	1.85	1.43
Tail	M	Adult.....	41	151.4-164.3	157.24±0.45	2.88	1.83
		First-year..	28	144.8-155.8	150.07±0.56	2.96	1.97
	F	Adult.....	37	142.1-153.8	146.73±0.50	3.04	2.07
		First-year..	17	138.3-149.5	144.12±0.73	3.03	2.10
Bill length	M	Adult.....	45	22.0- 25.7	23.51±0.14	0.96	4.08
		First-year..	25	21.2- 25.1	23.16±0.19	0.97	4.18
	F	Adult.....	37	20.0- 24.6	21.99±0.14	0.88	4.00
		First-year..	16	20.4- 23.1	21.59±0.17	0.68	3.15
Bill depth	M	Adult.....	43	10.1- 11.3	10.61±0.04	0.29	2.74
		First-year..	26	9.9- 11.1	10.49±0.06	0.29	2.76
	F	Adult.....	35	9.6- 11.0	10.12±0.06	0.33	3.26
		First-year..	13	9.4- 10.4	10.00		
Bill width	M	Adult.....	45	8.6- 10.3	9.32±0.06	0.37	3.97
		First-year..	26	8.5- 10.0	9.29±0.07	0.34	3.66
	F	Adult.....	38	8.6- 9.6	9.00±0.04	0.24	2.67
		First-year..	13	8.5- 9.6	9.05		
Tarsus	M	Adult.....	44	44.1- 48.0	46.07±0.13	0.88	1.91
		First-year..	28	44.8- 47.5	45.91±0.15	0.79	1.72
	F	Adult.....	39	41.3- 46.0	44.34±0.14	0.90	2.03
		First-year..	17	42.1- 45.9	44.53±0.21	0.87	1.95
Hind toe	M	Adult.....	45	13.0- 15.2	14.60±0.05	0.35	2.40
		First-year..	28	13.7- 15.0	14.42±0.07	0.37	2.56
	F	Adult.....	38	13.4- 14.8	14.01±0.06	0.37	2.64
		First-year..	17	13.4- 14.8	14.12±0.09	0.39	2.76
Middle toe	M	Adult.....	45	21.2- 23.0	22.00±0.07	0.49	2.23
		First-year..	27	20.9- 23.1	21.99±0.10	0.53	2.41
	F	Adult.....	39	20.2- 22.1	21.21±0.07	0.45	2.12
		First-year..	17	20.5- 21.8	21.06±0.09	0.38	1.80
Weights (gm.)	M	20	100 -147	124.7		
	F	17	100 -117	111.2		

Juvenal plumage: compared with *californica*, upper parts darker (Fuscous to Clove Brown); pileum tinged with darker and considerably more blue; superciliary line less extensive, reduced to a few streaks above and behind eye; sides of throat and chest darker (Chaetura Drab to Chaetura Black); under parts washed with slightly more pale brownish gray, including belly; under tail coverts and ankle feathers darker (dull gray); rectrices and remiges darker (Indigo Blue).

Geographic distribution.—Santa Cruz Island, off the coast of southern California.

Comparisons.—*Insularis* differs from all races of the "*californica*" group in intensity of coloration but not in pattern. *Obscura*, the darkest mainland race of the "*californica*" group, approaches *insularis* more closely than any of the others. First, the color of head and neck is approximately of the same shade of dark purplish blue, but that of *insularis* is more intense. Second, the under tail coverts are darker and consistently tinged in *insularis*, but are darker and more frequently tinged in *obscura* than in any other race of the "*californica*" group; the back of *obscura* is intermediate between that of *insularis* and that of *californica* or closer to the former; the lower breast and belly of *obscura* are similar to, or duskier than, those of *insularis*, but the anal region is more whitish than in *insularis*.

Differences in size between *insularis* and mainland races may be shown by comparing *insularis* with the largest mainland race of the "*californica*" group, *immanis* of the Willamette Valley; with the race of the neighboring mainland, *californica* of Santa Barbara and Ventura counties; and with the smallest race, *cactophila* of central Baja California. Corresponding measurements of these populations are shown in figure 8. The percentage differences are given in the table.

	<i>immanis</i>	<i>californica</i>	<i>cactophila</i>
Wing.....	+ 8.2	+13.1	+17.6
Tail.....	+11.3	+15.9	+22.8
Bill length.....	+21.2	+20.7	+25.1
Tarsus.....	+ 8.2	+16.4	+21.4

Variation.—Color differences between sex and age groups parallel those evident in *californica*; but among individuals of each group, variation is negligible in adult classes and slight in first-year groups. No extreme variants of the type evident in samples of mainland races from a given locality, such as the Monterey area, occur in the large series of *insularis* I have examined. In first-year females, blue coloration becomes less purplish (Dark Cadet Blue) than that of adult males of *obscura*, *californica*, and *oocleptica*, but not that of inland or more southern races. Variation in size parallels that of color. (See p. 363.)

Relationships of insularis to mainland forms.—Henshaw's (1886:452) early postulation of the origin of the dark, large scrub jay endemic to Santa Cruz Island probably represents the notion held by most ornithologists at the turn of the century. He suggested that vagrants from the mainland, "being non-migratory, took up residence" on the island. He was understandably puzzled by the dark coloration, which is more extreme than that of scrub jays from northern regions, in Oregon, with which he compared *insularis*. Further, he compared the color of under tail coverts with that of *woodhouseii*. *Insularis* certainly exceeds markedly all mainland races in size, but it is surprising to me that its close similarity in color to typical *obscura* from the Sierra San Pedro Mártir has never been noted. (See above.) It is not necessary to seek in the tinged under tail coverts of *woodhouseii*, as did Henshaw (1886:452) and others, any clue to the immediate relationships of *insularis*.

Dawson's (1920:28) theory of the origin of *insularis* does not differ fundamentally from that of Henshaw, although he attempts to provide a more complete picture than did Henshaw. Dawson states that the wings of *insularis* are "too short and weak to permit of its attempting a sheer flight of twenty-five miles" to or from the mainland. The shortest distance between Santa Cruz Island and the mainland is actually about twenty miles. There is a record of a scrub jay observed on the Farallon Islands (Gruber, 1884:172); these islands are slightly less than twenty miles from the nearest mainland. Local movements of scrub jays rarely include any

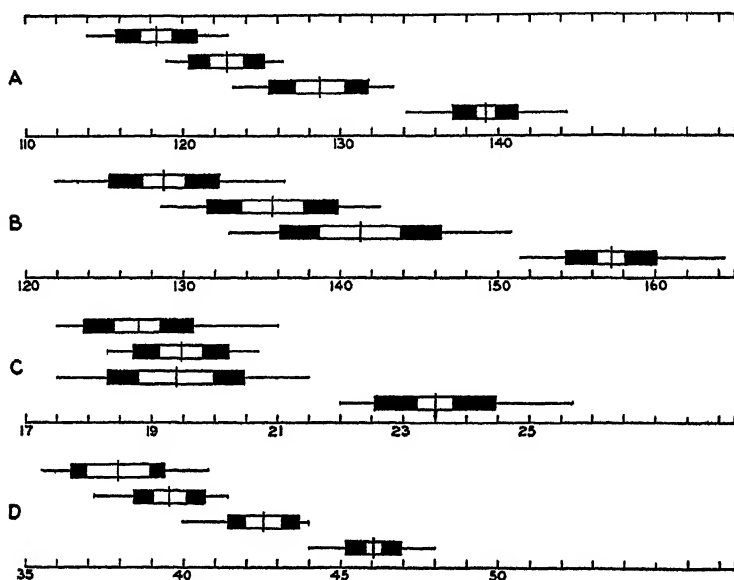


Fig. 8. Comparison of dimensions and individual variation of wing (A), tail (B), bill length (C), and tarsus (D) among races of "californica" group with special reference to *insularis* of Santa Cruz Island. Scales (mm.) are provided for each dimension. In each instance, data for four races are shown: from top to bottom, smallest mainland race, *coastophila* (table 15), *californica* of mainland opposite Santa Cruz Island (table 7), largest mainland race, *immanis* (table 23), and *insularis* (table 24).

but short flights; moreover, the humerus of *A. coerulescens* is relatively weak. Available evidence indicates that most individuals do not move far from their birthplace, and adults are sedentary. Thus the inherent tendency of first-year birds not to wander widely, and the sedentariness of adults together with, and at least partially interrelated with, a structural inadequacy of the wing, deter *insularis* from spreading. But the failure of *insularis* to spread at least to Santa Rosa Island to the west is puzzling (Cockerell, 1938a:181), unless environmental factors, such as prevailing winds, militate against this.

Dawson (1920:28) further suggested that the colonization of Santa Cruz "must have been assisted either by storm, or by drifting wreckage used as a refuge, or by human agency"; or else "migration occurred at a time when the channel which separates the island from the mainland was much narrower than at present." The

last suggestion is probably closer to the facts than any other explanation. According to Chaney and Mason (1934:21), a connection of Santa Cruz and neighboring islands with the mainland may have existed in the Pleistocene. The Pleistocene flora of Santa Cruz Island was similar to a coniferous type of forest existing today near Fort Bragg, Humboldt County, California (Chaney and Mason, *ibid.*:19). Scrub jays occur at the latter locality, not in association with the coniferous forest but with border vegetation, including such scrub genera as *Ceanothus*, *Arctostaphylos*, and *Garrya*, all recorded also from the Pleistocene of Santa Cruz Island. Thus there is evidence of a habitat on Santa Cruz Island during the Pleistocene suited to scrub jays as we know them today. Since scrub jays are recorded from the Pleistocene of the neighboring mainland (Miller, 1929:7, 1932:173, 1937:250), there is no reason to doubt the occurrence of the species on Santa Cruz Island at that time. But there is some doubt that the history of terrestrial vertebrates on the Santa Barbara Islands antedates the Pleistocene (Cockerell, 1938a:180, 1938b:6).

One of the fundamental questions in regard to *insularis* is, of course, the time during which differentiation of this distinctive form occurred. Cockerell (1939:311) suggested that "this bird acquired its distinctive features after the island became separated from the mainland," and concluded that "the evolution of the jay must be supposed to have occurred during a part of the Pleistocene." In the absence of conclusive evidence, one could suggest with equal justification that it was the mainland forms which underwent evolutionary change and that *insularis* is truly a "relict"; or, what is most likely, that *insularis* as well as mainland races have undergone change, apparently in opposite directions in size. I am inclined to regard the distinction of *insularis* in color as exaggerated by most authorities so far as its phylogenetic significance is concerned; comparison of *insularis* and *obscura*, as made above, seems to me to minimize that difference. What is needed is a careful study of fossil material of *Aphelocoma*. Miller (1937:250) identifies fossil species of *Aphelocoma* from the Pleistocene of the mainland as *A. c. californica*; this would indicate that the mainland forms were not markedly different in size from present-day forms. This, in turn, would support Cockerell's assumption, in part at least.

Few other endemic species or races of terrestrial vertebrates of the Santa Barbara Islands provide useful evidence of a kind parallel to that of the outstanding differentiation of the Santa Cruz Island scrub jay. As noted by Swarth (1918:418), among birds, "neither in trend taken by the characters serving to distinguish them from their mainland relatives, nor in the distribution of species upon the islands, is it possible to detect uniformity in the results attained."

There is no evidence from behavior that *insularis* differs in any important respect from mainland forms of the scrub jay. Observations in the period from August 28 to September 14, 1948, indicate that in variety and apparent function of call notes, and in flight, mannerisms, and reactions to features of habitat, *insularis* is similar to the scrub jays of the San Francisco Bay region (Pitelka, MS).

Mailliard (1899:42) considered the notes of *insularis* to be harsher than those of *californica*, approaching in quality those of *Cyanocitta stelleri*. Differences which I detected in certain call notes are of no greater order than those observed among different mainland populations. Compared to the call notes of *oocleptica*, those of

insularis differ in pitch only slightly. They are generally louder and harsher, a difference best associated with the difference in size. The magnitude of the difference, to my ear, is comparable to that between *oocleptica* of the Berkeley Hills and *obscura* of the Los Angeles region. The approach to the notes of *Cyanocitta stelleri* suggested by Mailliard (1899:42) is only slight.

I am aware of no fundamental difference in nidification between *insularis* and *californica*. In structure, the nest of *insularis* is, of course, bulkier than that of *californica*. Dawson (1920:28) has greatly labored the color characters of eggs of *insularis* as compared with those of mainland forms. It is popularly thought that the eggs are differently colored, but this is not so. Rather, the color of the eggs of mainland races varies rather strikingly from a reddish type to a greenish-blue type, the color terms referring to the light ground color. Eggs of *insularis* fall within this range of variation, but are more or less uniform in ground color, which is greenish blue, as well as in spotting, which is light. Although differences in dimensions between *insularis* and mainland races are striking, there is some tendency toward overemphasis or even exaggeration of these differences (Dawson, 1920:28). That the bill of *insularis* is relatively larger than that of mainland scrub jays (Murphy, 1938:538), however, is evident from the foregoing comparisons.

Ecologic distribution.—My observations on Santa Cruz Island indicated that in habitat requirements *insularis* resembles its mainland relatives. Among the varied forms of the woodland-chaparral complex of vegetation present on Santa Cruz Island and inhabited by scrub jays, essentially three types may be recognized.

1. The local areas of closed-cone pine forest (*Pinus remorata*, *P. muricata*), as at the upper end of west-facing Christy Canyon. Various shrubs, some of them tending in form toward small trees, occur in openings in the forest and intermixed with the trees. The chief species are *Photinia arbutifolia*, *Arctostaphylos tomentosa*, *Vaccinium ovatum*, *Quercus agrifolia*, *Q. tomentella*, *Comarostaphylis diversifolia*, *Ceanothus arboreus*, and *Diplacus aurantiacus*. At the forest edge, on drier sites and along the ridges, grow such shrub species as *Q. dumosa*, *Q. wislizenii*, and *Adenostoma fasciculatum*. This vegetation type is strongly reminiscent of the pine forests that occur on the Monterey peninsula.

2. Broad sclerophyll forest, very local and patchy in occurrence and here never even approaching forest stands except along Puerto Canyon opening onto the north shore at Prisoners Harbor. The chief species is *Quercus agrifolia*, represented by tall, often enormous and widely spreading individuals, occurring especially along bottoms of the larger interior canyons and in the canyons of the gentle north-facing slope near Prisoners Harbor. Other occasional species occurring with the live oak are *Q. macdonaldi*, *Prunus lyonii*, and *Photinia arbutifolia*, the last being the most common of the three. The oak groves are often bordered by, or to varying degree intermixed with, elements from the scrub woodland.

3. Scrub woodland, one of the chief vegetation types on the island as well as its most distinctive one. It consists of tall shrubs, each usually with several main stems, open below, with the result that a ground cover of grass and herbs is developed and occasionally also an understory of shrubs (*Symphoricarpos*). The canopy is usually 7 to 10 feet above the ground. The tall shrubs are in groves or so spaced that a person can move through the vegetation without difficulty; even when the

stand is relatively dense and the canopy fairly continuous, movement beneath the canopy among the stems is not greatly hindered. *Quercus wislizenii* and *Q. dumosa* are the chief dominants in this scrub woodland. Among the co-dominants are such species as *Photinia*, *Comarostaphylis*, *Arctostaphylos insularis*, *Cercocarpus alnifolius*, *Ceanothus arboreus*, *Ceanothus megacarpus* var. *insularis*, *Dendromecon harfordi*, and *Adenostoma fasciculatum*. These three habitat types are intermixed along the gentle north-facing slopes to the west of Prisoners Harbor.

Groves of ironwood (*Lyonothamnus floribundus*), typically present in rather deep draws at low and intermediate levels of the mountain slopes, are only local in distribution and do not figure importantly in habitat distribution of scrub jays. Where such groves occur, scrub jays move between them and the scrub woodland which is typically adjacent. Riparian woods of willows (*Salix lasiolepis*) and poplar (*Populus trichocarpa*) are local in distribution, even more so than the ironwood. They do not figure importantly in the habitat distribution of jays, although they are used wherever they occur. Large areas of grassland and an open vegetation of low shrubs (*Artemisia californica*, *Adenostoma fasciculatum*, *Eriogonum arborescens*, *Baccharis pilularis*, etc.) and cacti (*Opuntia*) with sparse herb cover or none at all represent important plant-cover types on Santa Cruz Island interposed between areas habitable for jays. The former is prominent near the east end of the island and the latter is extensively distributed on exposed slopes and high ridges.

Although jays were present in all areas of woodland, narrow-leaved or broad-leaved, deciduous or evergreen, they were least numerous in areas of scrub woodland on exposed, dry sites on the higher slopes and ridges. They were most common along canyon bottoms in the vicinity of groves of live oaks. In the latter situations, not only were adults most common, but young of the year were more or less concentrated, usually in small, loose flocks of four to six individuals. Along Puerto Canyon (see map, Bremner, 1932), habitat optimal for jays occurs and the species was present in what appeared to be maximal density. Along a portion of the canyon bottom where the live-oak woodland was more or less continuous, pairs of adults were spaced about 300 feet apart. This spacing is approximately similar to maximal densities of established pairs observed in mainland populations in the San Francisco Bay region (Pitelka, MS).

Foraging occurred on the ground and in canopies of trees such as oaks and *Prunus lyonii*. In the period of my observations, more foraging was done on the ground than within shrubs or trees. Jays were noted to feed on acorns of various species, nuts of the closed-cone pines, berries of *Vaccinium*, and drupes of *Prunus lyonii*.

Nests are recorded as having been placed in manzanita (*Arctostaphylos insularis*), Christmas berry (*Photinia arbutifolia*), cherry (*Prunus lyonii*), ironwood (*Lyonothamnus floribundus*), mountain mahogany (*Cercocarpus alnifolius*), closed-cone pines (*Pinus* spp.), live oaks (*Quercus agrifolia*), scrub oaks (*Q.* spp.), and willow (*Salix* spp.) (Beck, 1899:6; Howell and van Rossem, 1911:209; Willett, 1912:68; Dawson, 1921:61). Height of nest placement varies from 6 to 30 feet (Blake, 1887:329).

To my knowledge, no attempt has been made to estimate the population of in-

sularis. Dawson (1920:28) considered that the population totaled between 2,000 and 3,000 pairs. In my opinion this is a reasonable estimate. The island is about twenty-five miles long and eight miles wide at the widest point, but the species is not distributed over it uniformly.

Factors in the differentiation of insularis.—The fact that the scrub jay of Santa Cruz Island is the most striking insular differentiate among birds of the southern California islands especially whets one's curiosity about the factors which have effected that differentiation. First, with respect to color, my observations in late August and early September, when the main part of the population had completed or nearly completed the fall molt, provided no clue to the interpretation of its adaptive significance. In the live-oak groves and the pine forests, dark coloration appeared suited to the background afforded by dark foliage, and selection might be expected to favor dark coloration through the action of predators. But on the mainland, jays living in similar habitats, in Marin and Monterey counties, for example, are not dark-colored. Moreover, in scrub woodland, the most extensive of vegetation types occupied by the island jay and one of considerably lighter average coloration than the pine and live-oak habitats, the jays were conspicuous, often strikingly so. Finally, predators, at least in the summer and early fall seasons, are few. The only ones present that might take fully grown jays are the red-tail (*Buteo jamaicensis*) and the duck hawk (*Falco peregrinus*), but the populations of both of these are very sparse relative to that of the scrub jay. The red-tail is present in only a few scattered areas on the island; the duck hawk is more or less limited to the coast and adjacent rocky uplands. I doubt that the resident population of either of these species exceeds six or eight pairs. Thus the factor of predation, at least in summer and early fall, at present writing does not seem to me to be a critical one.

Predation may become critical in winter when Cooper hawks (*Accipiter cooperii*), pigeon hawks (*Falco columbarius*), and additional duck hawks occur on the island as migrants or winter visitants. At that time, under circumstances of increased predation, cloudiness along with persistent and extensive fogginess over the island, together with the vegetational background, may be the setting in which selection favors dark coloration. The only mainland race of the scrub jay that approaches the island race in darkness of coloration, *obscura* of the Sierra San Pedro Mártir, Baja California, also occurs in an area where fogs are supposedly frequent and widespread. No data are available on the seasonality of fogs and cloudiness, either on Santa Cruz Island or in the Sierra San Pedro Mártir, and it is therefore a question whether fogginess alone is significantly more prevalent in these areas than in mainland areas such as the San Francisco Bay region and the northern California coast.

It seems possible, though to my mind unlikely, that the present effect of selection on color in this insular race may be neutral. The climate and vegetation of Santa Cruz Island and the adjacent mainland in the Pleistocene resembled that of today in central and northern coastal California, and coloration of the parent populations from which *insularis* was derived may have become dark then. With subsequent isolation of the island population, and if predation has not been a critical factor since then, dark coloration may simply have persisted notwithstanding the spread of more xeric, lighter-colored vegetation types on the island.

The differential in size between mainland and island populations of the scrub jay is as striking as that in color. It seems possible that large size may be favored through differences in niche relationships of the island jay as contrasted with the mainland populations. Such differences would arise as a result of differences in the biotic structure of the two environments. A rough measure of these differences can be given by tabulating the breeding species of birds associated with chaparral and woodland vegetation on the mainland and the island, as is done in table 25. Among the small species, only three of a total of fourteen are absent on Santa Cruz

TABLE 25
BREEDING BIRDS CHARACTERISTIC OF CHAPARRAL AND (OR) WOODLAND
IN COASTAL CALIFORNIA

Size	Present on Santa Cruz Island and mainland	Absent on Santa Cruz Island, present on mainland
Small	<i>Calypte anna</i> <i>Selasphorus sasin</i> <i>Empidonax difficilis</i> <i>Psaltiriparus minimus</i> <i>Thryomanes bewickii</i> <i>Poliophtila caerulea</i> <i>Vireo huttoni</i> <i>Vermivora celata</i> <i>Spinus psaltria</i> <i>Aimophila ruficeps</i> <i>Spizella passerina</i>	<i>Parus inornatus</i> <i>Sitta carolinensis</i> <i>Chamaea fasciata</i>
Intermediate	<i>Zenaidura macroura</i> <i>Falco sparverius</i> <i>Colaptes cafer</i> <i>Balanosphyra formicivora</i> <i>Aphelocoma coerulescens</i> <i>Mimus polyglottos</i> <i>Carpodacus mexicanus</i> <i>Pipilo maculatus</i>	<i>Lophortyx californica</i> <i>Otus asio</i> <i>Phalaenoptilus nuttallii</i> <i>Dendrocopos nuttallii</i> <i>Myiarchus cinerascens</i> <i>Sialia mexicana</i> <i>Toxostoma redivivum</i> <i>Pheucticus melanocephalus</i> <i>Pipilo fuscus</i>
Large	<i>Buteo jamaicensis</i>	<i>Accipiter cooperii</i> <i>Bubo virginianus</i>

Island, whereas among twenty species of intermediate and large size, eleven are absent. Students familiar with the Californian avifauna may disagree about what species might be added or removed from table 25, but the point which it serves to support remains: of species which might be expected to occur in the chaparral-woodland environment of Santa Cruz Island, those of intermediate size are not so well represented as those of small size. This is not surprising, since insular faunas are typically depauperate, especially among larger, more wide-ranging species. But this feature of the avifauna of Santa Cruz Island may have special significance in the biology of the island scrub jay. This species is known to prey on eggs, nestlings, and possibly even adults of small passerines. At the same time, a number of

nonavian as well as avian predators present on the mainland are absent from the island. For a good many of these predators, small birds comprise only a variable portion of their prey, but in the collective absence of these predators, this source of food may be utilized by *insularis* more than it is by mainland races. If this is true, it would seem to me that large size would be favored in the island population. The circumstances on Santa Cruz Island, as now understood, appear to justify this hypothesis.

Another factor considered critical in the increased size of the island jay is that of vegetational structure. This factor is apparently not so much causal as it is permissive. The live-oak and pine woods are characteristically open. Neither pedal nor flight movements are hindered by density or continuity of branching and canopy or by density of stems and foliage close to the ground. This seems especially significant in the scrub woodland, the most extensive of the vegetation types occupied by the scrub jay. Its low stature and xeric character notwithstanding, this vegetation is open enough basally so that jays may progress rapidly, even flying beneath the canopy for at least short distances, whether in escape from a predator or in pursuit of prey. The correlation evident between certain characters of several mainland races and the type of vegetation prevalent in their respective ranges (see p. 366) lends support to the thesis. Thus the present evidence suggests that development of large size in the island jay is linked with the absence of certain "partial" competitors in the depauperate insular fauna and that this trend of differentiation has been permitted by the physical character of the vegetation and perhaps also by the factor of reduced predation on the jay itself. Presumably the rate at which this differentiation has occurred has been affected by the size of the population.

Increase in body size is not accompanied by a correlated increase in wing size, and the foregoing discussion is not intended to imply that the island jay spends more time in flight than its mainland relatives. Compared with *californica* of the central California coast, *insularis* is 28.0 per cent heavier in weight; wing and tarsus of *insularis* are, respectively, only 10.2 and 13.0 per cent longer. On the mainland, where size of wing in relation to body size is considered to reflect differences in amount of time spent on wing, wing length increases interiorward whereas body size decreases. Thus, increase in wing size in *insularis* is interpreted as a mere proportional accompaniment to the increase in body size and of itself without special adaptive significance.

THE "WOODHOUSEI" GROUP OF RACES

Apelocoma coerulescens woodhousei

Description and racial characters. Male: adult fall plumage.—Upper parts: pileum, hind neck, and sides of neck dull grayish blue (Tyrian Blue—Cadet Blue, or Dark Tyrian Blue—Dark Cadet Blue); auricular region brownish black, touched lightly with grayish blue; subauricular and suborbital regions grayish blue, as above, but slightly darker; lores grayish black, faintly and variably spotted with dull white; white, more or less irregular superciliary line, narrow anteriorly; back grayish brown (Hair Brown—Mouse Gray) suffused with dull blue; scapulars and rump more bluish gray (approaching Slate Blue—Delft Blue); upper tail coverts Tyrian Blue.

Under parts: chin, throat, and mid-chest dull white (Pallid Neutral Gray), seemingly streaked with gray, an effect due to absence of barbs from terminal portions of rachises, which become black on chin, together with variable graying of lateral margins of vanes; sides of chest dull

grayish blue; dull white feathers of chest edged laterally with dull grayish blue over a broad band, with little or no suggestion of a collar; median feathers of chest edged laterally with shade of blue duller than that of lateral feathers; lower breast light dull gray (Light Mouse Gray—Mouse Gray), becoming slightly darker on sides and lighter (Smoke Gray) toward crissum; anal region whitish; ankle feathers Light Mouse Gray, touched with pale blue; under tail coverts Light Windsor Blue—Pale Windsor Blue.

Wings and tail: remiges and feathers of alula dark grayish blue (Tyrian Blue, or Dark Tyrian Blue—Deep Orient Blue); primaries dull dark brown (Fuscous) distally; inner webs of all remiges except innermost secondaries similar in color; fifth primary longest; innermost secondaries and coverts (especially marginal coverts) of slightly brighter blue (Tyrian Blue—Deep Orient Blue); under wing coverts dull gray (Mouse Gray), becoming dull blue near wing margin; rectrices similar to remiges in color (Dark Tyrian Blue—Deep Orient Blue). Wing-tail ratio, 0.910:1. (See table 26 for other statistical data.)

Bill: black, heavy; hook reduced or lacking; bill tapering, more or less pointed; culmen convex with slight or no increase in curvature distally.

Feet: black.

Iris: brown.

Sex and age differences in color and size closely parallel those of *californica*.

Male and female: juvenal plumage.—Upper parts: pileum, hind neck, suborbital and auricular regions, sides of upper chest, and upper tail coverts Hair Brown; pileum tinged usually and in varying degree with dull blue; back, scapulars, and wing coverts (but not greater wing coverts) similar or lighter (Hair Brown, tending toward Drab); superciliary line narrow, irregular, and short, dull brownish white, reduced or lacking in supra-auricular area.

Under parts: chin and throat dull white; sides of throat and chest dull grayish brown (light Drab to Mouse Gray), forming broad, indistinct band across chest, upper parts of which, along lower edge of throat area, are white with lateral margins of feathers Light Drab; lower breast and belly dull gray (Smoke Gray), approaching white around anal region; under tail coverts and ankle feathers darker (Mouse Gray).

Wings and tail: remiges duller than in adults (Delft Blue—Deep Delft Blue); distal portions of primaries and inner webs of all except innermost remiges dull dark brown, slightly lighter than in adults; middle and marginal coverts dull brown (Hair Brown), middle coverts tinged distally with dull blue; greater wing coverts and feathers of alula similar to remiges, but tipped with dull brown; rectrices similar to remiges in color.

Bill and feet: varying shades of brown and brownish black, depending on age.

Individual, age, and sex variation.—Variation in *woodhouseii* due to individual, age, or sex differences parallels that evident in *californica* in every way. Additional details set forth here concern primarily the specific limits of color variation in *woodhouseii*. Since the "*woodhouseii*" group of races is the second largest in the *coerulescens* complex, and since evidence of parallelism in size variation is available from comparisons of tables of dimensions, it seems desirable to record the corresponding data on color.

Among adult males the color of the pileum is typically Tyrian Blue—Cadet Blue or slightly darker. Darker variants reach Dark Tyrian Blue—Dark Cadet Blue (C 114454, Kenton); few specimens show a color duller or lighter than the typical one, and these are closest to Tyrian Blue—Dark Tyrian Blue (C 114453, Kenton). Blue of under tail coverts is typically Light Windsor Blue—Pale Windsor Blue. Dark variants reach Light Tyrian Blue (MCZ 315641, Garfield County); light ones reach Pale Windsor Blue, with the blue reduced, as in females (C 113225, Kenton).

In first-year males, blue coloration varies more than in adult males. Certain individuals are as darkly colored as dark adults, approaching Dark Tyrian Blue—

TABLE 26

MEASUREMENTS OF *A. C. WOODHOUSEII* FROM COLORADO, EASTERN UTAH, NORTHEASTERN ARIZONA, AND NORTHERN NEW MEXICO

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	50	125.0-136.8	130.92±0.40	2.85	2.18
		First-year..	39	124.2-133.6	129.36±0.39	2.46	1.90
	F	Adult.....	26	120.9-131.0	126.46±0.50	2.53	2.00
		First-year..	28	119.0-123.3	123.43±0.39	2.08	1.68
Tail	M	Adult.....	48	134.0-151.9	143.94±0.60	4.17	2.90
		First-year..	37	131.7-145.0	138.95±0.55	3.34	2.41
	F	Adult.....	25	126.3-144.5	136.76±0.84	4.21	3.08
		First-year..	21	125.0-139.3	132.90±0.90	4.13	3.10
Bill length	M	Adult.....	49	18.2- 22.9	19.93±0.13	0.88	4.40
		First-year..	31	17.0- 21.7	19.51±0.17	0.96	4.93
	F	Adult.....	37	17.0- 20.8	19.06±0.18	0.91	4.78
		First-year..	20	17.5- 20.9	18.61±0.18	0.81	4.34
Bill depth	M	Adult.....	48	7.9- 9.5	8.57±0.06	0.40	4.66
		First-year..	31	7.4- 9.2	8.44±0.08	0.46	5.45
	F	Adult.....	25	7.5- 8.7	8.22±0.07	0.34	4.16
		First-year..	20	7.4- 9.0	8.15±0.08	0.35	4.25
Bill width	M	Adult.....	48	7.5- 8.9	8.12±0.05	0.33	4.04
		First-year..	31	7.5- 8.8	8.03±0.07	0.39	4.88
	F	Adult.....	27	7.2- 8.7	7.95±0.07	0.35	4.40
		First-year..	20	7.1- 8.5	7.90±0.09	0.39	4.94
Tarsus	M	Adult.....	49	37.0- 42.9	39.71±0.16	1.10	2.78
		First-year..	39	36.1- 42.4	39.73±0.21	1.32	3.32
	F	Adult.....	26	37.1- 41.0	39.10±0.21	1.08	2.76
		First-year..	28	35.8- 40.9	38.46±0.22	1.19	3.09
Hind toe	M	Adult.....	50	11.2- 13.8	12.37±0.08	0.58	4.66
		First-year..	39	11.1- 13.4	12.27±0.09	0.55	4.45
	F	Adult.....	27	11.3- 13.5	12.19±0.08	0.44	3.62
		First-year..	28	11.1- 12.6	11.87±0.07	0.38	3.21
Middle toe	M	Adult.....	50	17.2- 20.4	18.67±0.11	0.74	3.98
		First-year..	38	17.1- 20.1	18.57±0.12	0.75	4.05
	F	Adult.....	25	17.3- 19.1	18.26±0.10	0.49	2.68
		First-year..	26	16.8- 19.2	17.93±0.12	0.59	3.31

Deep Cadet Blue (CO 13622, Denver); others are as dark but duller, being Dark Tyrian Blue—Tyrian Blue (KU 20814, twelve miles northeast of Elkhart). Most specimens are slightly lighter, usually Tyrian Blue (CO 13620, Sedalia), or Tyrian Blue—Dark Tyrian Blue (CM 2333, Fort Lyon). Under tail coverts vary in color as in adults, some individuals (CO 13620) being as richly colored as the darkest adults; but the number of variants of the duller, grayer extreme are much more numerous. Thus the average color is duller and grayer.

TABLE 27

MEASUREMENTS OF *A. C. WOODHOUSEII* FROM SOUTHERN NEW MEXICO AND WESTERN TEXAS

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	18	124.1-132.2	128.67±0.50	2.11	1.64
		First-year..	15	123.4-130.3	126.60		
	F	Adult.....	19	120.4-127.4	123.32±0.42	1.84	1.49
		First-year..	8	118.0-125.5	121.63		
Tail	M	Adult.....	17	136.0-147.3	141.65±0.74	3.07	2.17
		First-year..	15	128.3-143.3	135.60		
	F	Adult.....	18	126.0-137.1	132.33±0.76	3.25	2.45
		First-year..	8	122.5-132.1	127.50		
Bill length	M	Adult.....	18	17.6- 21.6	19.73±0.25	1.06	5.40
		First-year..	16	17.6- 20.8	18.91±0.21		
	F	Adult.....	19	16.5- 20.7	18.41±0.24	1.05	5.73
		First-year..	8	17.5- 19.4	18.48		
Bill depth	M	Adult.....	17	8.4- 9.0	8.66±0.06	0.24	2.79
		First-year..	15	7.9- 9.5	8.52		
	F	Adult.....	19	7.5- 8.8	8.17±0.07	0.31	3.84
		First-year..	8	7.2- 8.9	8.35		
Bill width	M	Adult.....	18	7.3- 9.4	8.46±0.12	0.49	5.81
		First-year..	16	7.8- 9.2	8.38±0.09		
	F	Adult.....	19	7.1- 8.9	8.11±0.11	0.50	6.16
		First-year..	8	7.5- 8.2	8.07		
Tarsus	M	Adult.....	18	37.9- 41.1	39.79±0.20	0.87	2.18
		First-year..	16	37.7- 41.1	39.73±0.22		
	F	Adult.....	19	37.1- 40.3	38.85±0.24	1.04	2.68
		First-year..	8	37.4- 40.7	38.97		
Hind toe	M	Adult.....	18	11.6- 12.8	12.23±0.09	0.37	3.07
		First-year..	16	11.9- 13.1	12.43±0.09		
	F	Adult.....	19	11.1- 12.9	12.03±0.11	0.47	3.91
		First-year..	8	11.0- 12.5	11.83		
Middle toe	M	Adult.....	18	16.9- 20.0	18.68±0.18	0.79	4.21
		First-year..	16	17.8- 19.6	18.66±0.15		
	F	Adult.....	19	16.6- 20.2	18.16±0.17	0.76	4.20
		First-year..	8	17.1- 18.9	18.14		

In adult females, color in the pileum is typically Tyrian Blue—Cadet Blue (C 113210, Kenton; MCZ 151574, Colorado Springs). Darker variants reach Dark Tyrian Blue—Tyrian Blue (AM 49913, Folsom); lighter variants reach Tyrian Blue (AM 372183, Newcastle). First-year females average lighter and duller than adults, and are typically Tyrian Blue (C 114443, Kenton). Blue color of under tail coverts in both adult and first-year females is replaced to varying degrees with gray, although not completely; the blue varies in intensity among different specimens from Columbian Blue—Light Columbian Blue to Cadet Gray.

Variation in color of the back is negligible. With the exception of the blue coloration of the collar and under tail coverts, this is also true of under parts. Differences in color of collar, wings, and tail parallel those of head and neck.

Geographic distribution.—Rocky Mountains and neighboring regions, from southern Wyoming (McCreary, 1939:67) and north-central Utah (Ogden) south to southern New Mexico (Florida Mountains, Las Cruces) and western Texas (Glass Mountains; twenty miles southwest of Marathon), west to central Utah (Salt Lake City, Fish Lake, Navajo Mountain), northeastern Arizona (Keam Canyon, nineteen miles southwest of Kayenta), and southwestern New Mexico (Reserve, Florida Mountains), east to north-central (Boulder County) and southeastern (Bent and Las Animas counties) Colorado, extreme western Oklahoma (Kenton), eastern New Mexico (Folsom, Las Vegas, Guadalupe Mountains), and western Texas (Glass Mountains; twenty miles southwest of Marathon).

In southern Wyoming the status of the scrub jay appears to be that of an irregular visitant. Reported dates of occurrence (McCreary, 1939:67) are for August and October only. To my knowledge, the only evidence of nesting in that state is the statement of Knight (1902:107) that "Aiken found them nesting near Sherman," Albany County, southeastern Wyoming.

On the east side of the Rocky Mountains in Colorado, in the lower valleys and along the edge of the plains, scrub jays occur as migrants or irregular visitants in the nonbreeding seasons (Cooke, 1897:90; Bergtold, 1917:123; Lincoln, 1920:69). The available marginal records are Barr Lake, Adams County (Hershey and Rockwell, 1909:118), Fort Lyons, Bent County (Cooke, 1897:90), and extreme northwestern Baca County (Cary, 1909:182). Vagrant individuals probably reach points farther east; there is one record for North Platte, Nebraska (Bruner, 1898:121). In the southwestern corner of Kansas (Morton County), Long (1935:240) obtained specimens of scrub jays of the race *woodhousei* in November. Four of these, apparently taken by his field party (KU 20812-5, twelve miles northeast of Elkhart), have been examined by me; they prove to be first-year birds. There is no evidence that scrub jays breed there, although they are known to do so not far to the south in extreme western Oklahoma (Nice, 1922:181). In the Texas Panhandle, in late September, Stevenson (1942:114) observed four scrub jays southwest of Claude, Armstrong County, and several individuals along the Canadian River north of Amarillo, Potter County. The records from the areas under discussion here suggest that the scrub jay would be found to be an irregular, although not rare, visitant over most of them, were they to receive more attention from ornithologists.

In western Texas it is probable that the distributional area of *woodhousei* is larger than that suggested above, where the cited localities are based upon examined specimens. Scrub jays have been reported to the south and west of those localities, in the Chisos and Chinata mountains, respectively (Oberholser, 1920:91). (See fig. 10.)

Evidence of migration in the scrub jay is most clear cut in the race *woodhousei* and is provided mainly by the data of early observers in Colorado. Their fall, winter, and spring records of scrub jays along the lower eastern edges of the Rocky Mountains and on the bordering plains indicate a post-breeding dispersal to lower

elevations. The species breeds at elevations of 5,000–8,000 feet (Cooke, 1897:90; Bailey, 1928:477), being commonest at about 6,000 feet. In northern Utah the vertical range is reported as 6,500–8,000 feet (Twomey, 1942:419); in the Navajo Mountain area of southern Utah, 4,500–7,000 feet (Woodbury and Russell, 1945:

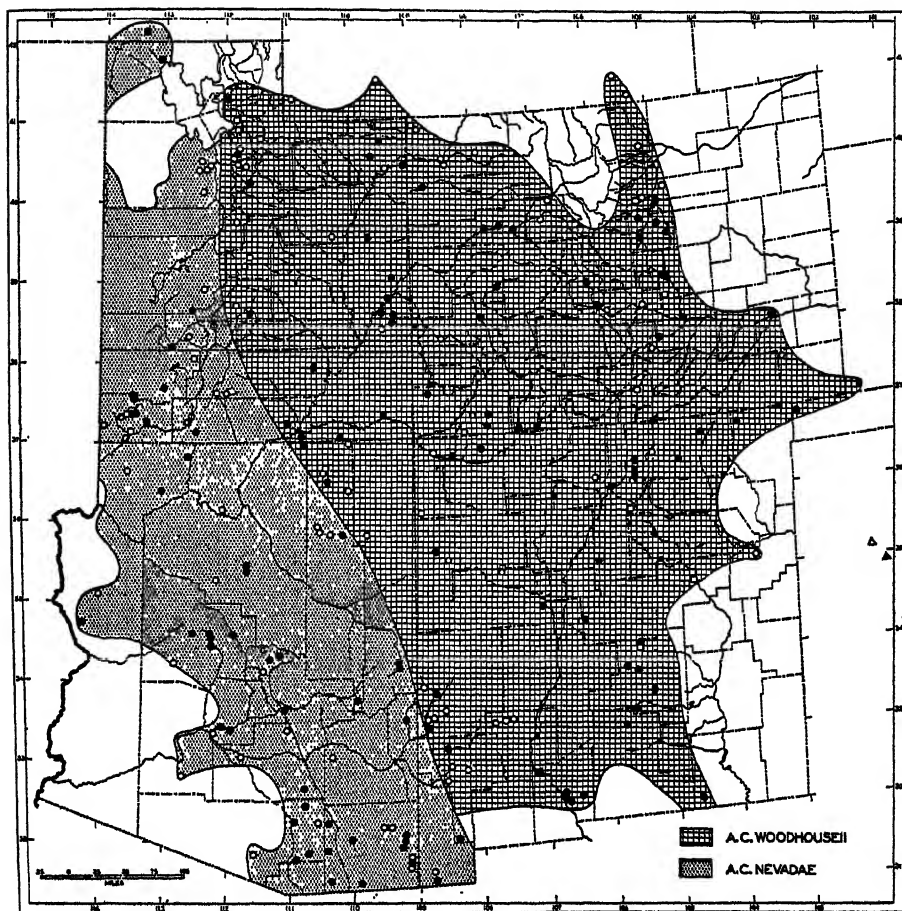


Fig. 9. Distribution of races of *Aphelocoma coerulescens* in Utah, Arizona, Colorado, and New Mexico. Dots indicate localities from which specimens have been examined; circles, localities reported in the literature; squares, type localities; triangles, vagrants.

86); but in western Texas scrub jays are said to occur chiefly at elevations below 6,000 feet (Burleigh and Lowery, 1940:115). After the breeding season, scrub jays may wander to elevations above the breeding range to 9,500 feet (Cooke, 1897:90; Rockwell, 1907:81). The subsequent movement to lower elevations is more or less sporadic, and the extent of this movement appears to vary from year to year, judging by the fact that most observers comment on infrequency or irregularity in the occurrence of this species. Of specimens taken at localities not near breeding grounds, all prove to be first-year birds. Moreover, not all individuals

participate in these migratory movements: Aiken and Warren (1914:536) reported Aiken's observation, in October, 1873, of a large number of scrub jays passing over an area on which locally established individuals were to be found throughout the year. (See also Rockwell, 1908:168.) In southern Utah (Woodbury

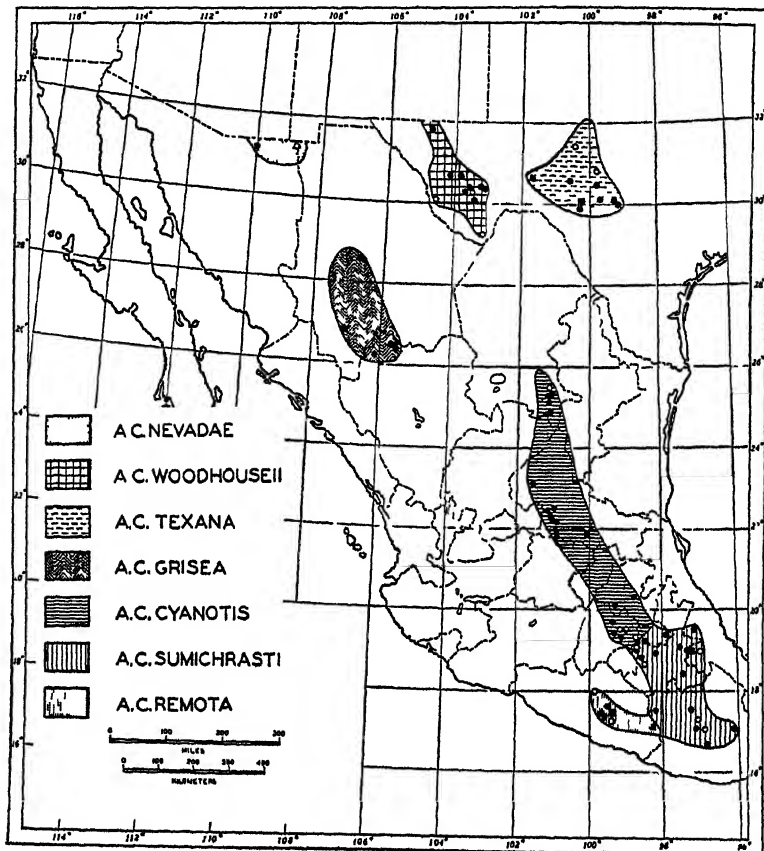


Fig. 10. Distribution of races of *Aphelocoma coerulescens* in Texas and Mexico. Dots indicate localities represented by specimens; circles, localities reported in the literature; squares, type localities. *A. coerulescens* is now known to occur farther south on the west side of the plateau than shown above (see text).

and Russell, 1945:86), New Mexico (Bailey, 1928:477), and western Texas (Burleigh and Lowery, 1940:115), most individuals apparently remain on the breeding grounds. The period of time over which fall movements take place is not known, but apparently they do not necessarily continue into the winter, as wintering flocks or individuals may stay at one locality from November until April (Aiken and Warren, 1914:536; see also Cooke, 1897:90). It is my impression that most, if not all, of the scrub jays which have been recorded appreciable distances from breeding grounds are first-year birds and that adult birds remain for the most part close to, if not actually on, their respective breeding areas. Rockwell (1908:81) regards

food supply as a more important factor in the migration of scrub jays than climatic conditions; while this may be so, he was not aware of any differences between first-year and adult birds with respect to migration or dispersion. I would suggest that the greater part of the observed, so-called migratory movements of this species represents the dispersal of birds of the former age group.

From this discussion, several questions bearing upon the general problem of migration suggest themselves. If, as is suggested above, winter visitants on the plains border of eastern Colorado are all first-year birds, the movements of these birds do not, strictly speaking, represent migratory movements but rather a dispersal which is suggestive of migration to lower elevations because of adverse conditions at higher elevations. The fact that locally established birds may remain on breeding grounds lends support to this notion. Yet the possibility of migration, in this instance partial migration, remains, and only careful observation of local populations and banding studies can clarify these problems. Comparable problems are presented by *Cyanocitta stelleri*, again in mountainous areas, and by *C. cristata* in eastern states (Pitelka, 1946b), where actual migration of the latter species may extend more than a thousand miles.

Although evidence of post-breeding movements within the breeding range of *woodhouseii* includes no records of long distances, as does that from the eastern periphery of the range, there is no reason to doubt that dispersal and migration of comparable degree occur, especially in the more northern parts of the range, as in western Colorado and Utah. Fall and winter occurrences of scrub jays at elevations below the breeding range have been recorded in southwestern Colorado (Gilman, 1907:155), western Colorado (Rockwell, 1907:81), and northern Utah (Hayward, 1935:282; Twomey, 1942:419). Nowhere within the range of *woodhouseii* is there evidence of a general vertical movement; rather, the winter movements of this species are sporadic and irregular, with the result that their numbers at localities below the breeding range vary rather noticeably from place to place and from year to year.

Comparisons.—The detailed description of "*woodhouseii*" serves as a basis for the characterization of all other races of the *woodhouseii* group, which are otherwise compared only with neighboring races.

Geographic variation and intergradation.—The characters ascribed to *woodhouseii* are seen in specimens from south-central Colorado, northern New Mexico, and extreme western Oklahoma and southwestern Kansas. Intergradation of *woodhouseii* and *nevadae* occurs westwardly. (See p. 291.)

Southward, in western Texas, *woodhouseii* intergrades with *texana*. In the main, specimens from that region are similar or closest to *woodhouseii*; compared with *texana*, they exhibit duller, less purplish-blue areas, lighter backs overcast with more blue or blue gray, and darker under tail coverts. An examination of individual color characters, however, reveals a small but appreciable percentage of specimens with characters of *texana*. In color of pileum and back, both lighter in *woodhouseii* than in *texana*, the majority of specimens are similar to *woodhouseii*; a few are closer or similar to *texana* (table 28). In color of under parts, however, the majority are similar to *texana*. In color of under tail coverts, approximately 50 per cent ("white" and "light" of table 28) are comparable to *texana*; the others are closer or similar to *woodhouseii*.

Among the intergrades, characters of the two races may be mixed variously. Individual specimens may approach *texana* in most characters, *woodhouseii* in others, or vice versa. Thus, under parts of one example, an adult male (CM 70614), are typical of *texana*; blue areas are slightly lighter, but closest to that race, whereas the back is light as in *woodhouseii*. Two other examples (BS 184241, 194243), collected in August, although molted incompletely, appear to be similar to *wood-*

TABLE 28

VARIATION IN SELECTED COLOR CHARACTERS OF SCRUB JAYS FROM WESTERN TEXAS COMPARED WITH *TEXANA* AND TYPICAL *WOODHOUSEII*

	Sex	Age group	Light	Intermediate	Dark	Total specimens	
-WOODHOUSEII							
Pileum	M	Adult.....	8	1	0	9	
		First-year.....	5	0	2	7	
	F	Adult.....	5	0	0	5	
		First-year.....	7	0	0	7	
Back	M	Adult.....	7	..	0	7	
		First-year.....	4	..	1	5	
	F	Adult.....	4	..	0	4	
		First-year.....	7	..	0	7	
	Sex	Age group	White	Light	Inter- mediate	Dark	Total specimens
WOODHOUSEII-							
Under parts	M	Adult.....	..	12	3	1	16
		First-year.....	..	4	1	1	6
	F	Adult.....	..	8	3	0	11
		First-year.....	..	7	0	1	8
Under tail coverts	M	Adult.....	2	5	5	4	16
		First-year.....	1	1	1	4	7
	F	Adult.....	3	4	4	1	12
		First-year.....	2	4	1	1	8

houseii in all characters except color of under tail coverts, which are light or whitish. Examples of typical *woodhouseii* (LU 2073) may be selected in the series from western Texas, but none approaches *texana* more closely than specimen CM 70614. Of special interest, however, are certain variants which depart from both *woodhouseii* and *texana*. The under parts of one, and the under tail coverts of the same and another specimen (LU 2563, UM 98911, respectively), are unusually dark, reaching Tyrian Blue. These variants might be interpreted as the result of combined hereditary effects of the heavier pigmentation of under parts and under tail coverts of *woodhouseii* and the generally richer coloration of *texana*. It is noteworthy that among specimens of a race neighboring *woodhouseii* to the southeast,

cyanotis, there are variants in a series from southeastern Coahuila which are even darker than those peculiar to western Texas, although they are not intergrades, since typical *cyanotis* is, in general, lighter than *woodhouseii*. Little more can be said of this interesting situation until more specimens are obtained from various parts of western Texas and Coahuila.

In size, there are statistically significant but small differences between specimens from western Texas and southern New Mexico (table 27), and typical *wood-*

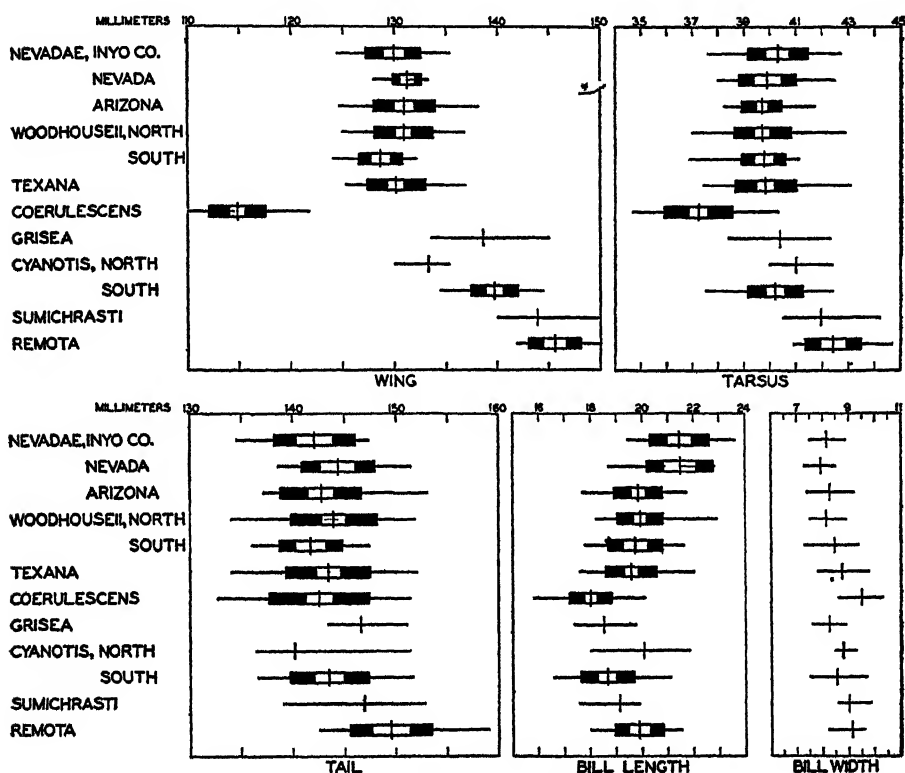


Fig. 11. Individual and geographic variation in races of *Aphelocoma coerulescens* of Great Basin, Rocky Mountains, Florida, and Mexico. Data arranged in north-to-south and east-to-west order, and based on adult males.

houseii (table 26) in average lengths of wing and tail, which are shorter in the former. Differences in bill dimensions are statistically negligible when corresponding groups of tables 26 and 27 are compared; but differences, however slight, are consistent in direction from one group to another in all instances except bill depth in adult females. From this comparison it is seen that the bill of southern representatives of *woodhouseii* tends to be shorter and basally heavier, thus displaying a trend toward *texana* (table 32), although remaining closer to *woodhouseii*.

Ecologic distribution.—In the breeding season, scrub jays of the race *woodhouseii* inhabit woodland and chaparral associations of more or less open, or at least broken, and scrubby aspect. They occur characteristically in woodlands of piñon (*Pinus*

edulis) and juniper (*Juniperus monosperma* and *J. scopulorum*) and in thickets of broad-leaved shrubs such as scrub oaks (*Quercus* spp.), manzanita (*Arctostaphylos*), *Ceanothus*, serviceberry (*Amelanchier*), and hackberry (*Celtis* spp.). Preference is shown for areas interspersed with openings and for borders of brushy ravines and wooded creek bottoms (Coues, 1874b:220; Bailey, 1904:335; Aiken and Warren, 1914:536; Behle, 1941:182; Twomey, 1942:419). The location of 26 nests found in Utah was as follows: in oaks, 16; in skunkbush (*Rhus*), 5; in squawbush (*Rhus*), 1; in cottonwoods, 2; in sagebrush, 1; in willows, 1; nest height was usually 3 to 6 feet above the ground, and rarely as low as 18 inches (Woodbury, Cottam, and Sugden, MS). Woodbury and Russell (1945:87) regard scrub jays of the Navajo Mountain region as primarily associated with oak chaparral, although they occur also in piñon-juniper woodland and in other types of brush or thicket; there the piñon-juniper woodland is inhabited by the piñon jay, the scrub jay occurring in largest numbers in chaparral at somewhat higher elevations. (See also Hayward, 1948:498, 499.) It may occur also in areas of yellow pine interspersed with scrub oak (Woodbury, Cottam, and Sugden, MS).

In western Texas the habitat of *woodhouseii* is characterized by such plant species as piñon (*Pinus edulis*), juniper (*Juniperus gymnocarpa* and *J. pachyphloea*), madrone (*Arbutus texana*), catclaw (*Mimosa biuncifera*), and wild plum (*Prunus virens*) (Burleigh and Lowery, 1940:90). In extreme western Oklahoma, *woodhouseii* is confined to an association of piñons, junipers (*J. monosperma*), and scrub oaks (Nice, 1922:181).

In fall and winter, scrub jays occur in wooded canyons and river-bottom thickets at elevations below the breeding range (Bailey, 1928:477; Twomey, 1942:419; Woodbury and Russell, 1945:87). Over certain parts of eastern Colorado and the panhandle of Texas, areas of juniper (*J. monosperma*) are inhabited by scrub jays in winter (Cary, 1909:182; Stevenson, 1942:114), but apparently they do not breed there. Winter occurrences are also reported from areas of desert scrub in which such species as greasewood (*Larrea tridentata*), catclaw (*Mimosa biuncifera*), or mesquite (*Prosopis glandulosa*) are dominant (Burleigh and Lowery, 1940:90, 115; Stevenson, 1942:114). Post-breeding movements into plant associations at higher elevations also occur; Woodbury and Russell (1945:87) record a July-taken immature female from an area of yellow pine and aspen on Navajo Mountain at 8,500 feet.

Aphelocoma coerulescens nevadae

Racial characters.—Differs from *woodhouseii* chiefly in color; pileum, hind neck, and sides of head of lighter and duller (less purplish) blue (Tyrian Blue—Deep Orient Blue); back duller (less brownish), suffused with more gray or blue gray; under tail coverts lighter (Columbian Blue—Light Columbian Blue, or Columbian Blue—Cadet Gray). Bill longer, more pointed and tapering; percentage difference in bill length of adult males, +7.6. Wing-tail ratio, 0.915:1. (See also table 29.)

Juvenal plumage similar to or slightly lighter than that of *woodhouseii*. (See discussion, p. 294.)

Geographic range.—Principally the Great Basin and Arizona; southeastern Oregon (Andrews) and southern Idaho (Cassia) south to the Providence Mountains, California, southern Nevada (Potosi Mountain, Virgin Mountains), west-

TABLE 29

MEASUREMENTS OF A. C. NEVADAE FROM DESERT RANGES

BORDERING CALIFORNIA-NEVADA LINE

(Mono and Esmeralda Counties South to San Bernardino and Clark Counties)

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.	24	124.5-135.4	130.00±0.54	2.66	2.04
		First-year..	19	123.3-131.5	127.63±0.48	2.08	1.63
	F	Adult.	11	120.0-128.9	123.82		
		First-year..	15	116.0-124.4	121.20		
Tail	M	Adult.	20	134.6-147.3	142.10±0.89	3.98	2.80
		First-year..	18	132.0-145.6	138.94±0.95	4.05	2.89
	F	Adult.	10	126.0-144.0	133.30		
		First-year..	12	123.5-136.1	130.00		
Bill length	M	Adult.	26	19.4- 23.6	21.44±0.23	1.15	5.38
		First-year..	13	18.9- 23.4	21.12		
	F	Adult.	13	19.1- 21.3	20.34		
		First-year..	11	17.6- 20.6	19.33		
Bill depth	M	Adult.	26	7.8- 9.3	8.70±0.07	0.38	4.35
		First-year..	12	7.5- 8.8	8.28		
	F	Adult.	13	7.6- 8.6	8.11		
		First-year..	11	7.0- 8.5	7.83		
Bill width	M	Adult.	26	7.5- 8.9	8.13±0.08	0.40	4.90
		First-year..	13	7.2- 8.5	7.90		
	F	Adult.	13	7.1- 8.4	7.87		
		First-year..	11	7.2- 8.5	7.70		
Tarsus	M	Adult.	26	37.6- 42.7	40.31±0.23	1.16	2.89
		First-year..	19	37.8- 42.0	39.60±0.27	1.19	3.02
	F	Adult.	13	36.3- 40.2	38.65		
		First-year..	15	36.2- 40.3	38.66		
Hind toe	M	Adult.	26	11.8- 14.3	12.67±0.11	0.55	4.38
		First-year..	19	11.2- 13.6	12.51±0.11	0.48	3.87
	F	Adult.	13	10.8- 14.1	12.11		
		First-year..	15	11.4- 12.5	12.06		
Middle toe	M	Adult.	26	18.1- 20.8	19.16±0.11	0.58	3.06
		First-year..	19	17.3- 20.3	18.56±0.19	0.81	4.39
	F	Adult.	13	16.8- 18.9	17.99		
		First-year..	15	17.0- 19.7	17.90		
Weights (gm.)	M	33	69 - 98	81.1		
	F	23	67 - 79	72.5		

TABLE 30

MEASUREMENTS OF *A. C. NEVADAE* FROM NEVADA EXCLUSIVE OF SOUTHWESTERN PORTION
BORDERING CALIFORNIA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	17	128.1-133.3	131.20±0.34	1.41	1.07
		First-year..	19	123.4-132.3	128.11±0.48	2.10	1.64
	F	Adult.....	10	121.6-127.2	125.60		
		First-year..	10	117.8-126.3	122.10		
Tail	M	Adult.....	17	138.5-151.4	144.35±0.87	3.58	2.48
		First-year..	18	129.8-145.5	138.56±0.91	3.88	2.80
	F	Adult.....	8	132.4-142.9	137.13		
		First-year..	9	125.0-138.3	130.67		
Bill length	M	Adult.....	16	18.7- 22.8	21.48±0.32	1.29	6.02
		First-year..	10	18.9- 22.2	20.38		
	F	Adult.....	12	18.8- 21.9	20.20		
		First-year..	11	18.7- 20.6	19.46		
Bill depth	M	Adult.....	16	8.1- 9.4	8.70±0.09	0.37	4.28
		First-year..	9	8.0- 9.2	8.47		
	F	Adult.....	12	7.7- 8.7	8.15		
		First-year..	11	7.3- 8.4	7.89		
Bill width	M	Adult.....	16	7.3- 8.5	7.92±0.09	0.38	4.80
		First-year..	10	7.4- 8.6	7.93		
	F	Adult.....	12	6.3- 8.2	7.75		
		First-year..	11	7.0- 7.8	7.54		
Tarsus	M	Adult.....	16	38.0- 42.5	39.91±0.28	1.10	2.77
		First-year..	11	38.2- 41.6	39.96		
	F	Adult.....	12	36.4- 41.3	38.65		
		First-year..	12	36.9- 40.2	38.47		
Hind toe	M	Adult.....	16	11.5- 13.0	12.39±0.11	0.42	3.41
		First-year..	20	12.2- 13.3	12.68±0.08	0.33	2.63
	F	Adult.....	12	11.4- 13.0	12.33		
		First-year..	12	11.2- 13.0	12.08		
Middle toe	M	Adult.....	16	16.9- 20.4	18.87±0.24	0.97	5.15
		First-year..	20	18.1- 19.7	18.94±0.10	0.47	2.49
	F	Adult.....	12	16.2- 18.9	18.00		
		First-year..	12	16.7- 19.5	18.28		
Weights (gm.)	M	7	75 - 97	83.8	} Northern Nevada	
	F	5	71 - 83	76.4		
	M	10	75 - 85	79.3	} Southern Nevada	
	F	9	65 - 78	72.5		

central Arizona (Chemehuevi Mountain), southeastern Arizona (Baboquivari Mountains, Sutton and Phillips, 1942:62), and extreme southwestern New Mexico (San Luis Mountains); west to western Nevada (Quinn River Crossing, Pine Grove) and east-central California (Williams Butte, White, Inyo, and Argus mountains); east to Utah (Kelton, Cove Fort, ten miles north of Kanab), northeastern Arizona (Keam Canyon, Springerville), and southwestern New Mexico (Sierra Hachita). Southward, scrub jays, probably of the race *nevadae*, range into northeastern Sonora (van Rossem, 1945:172).

Certain marginal records of scrub jays may represent sporadic wandering beyond their normal range rather than the periphery of that range. Two August records from southeastern Oregon reported by Gabrielson and Jewett (1940:423) are the only records of *nevadae* for that state; one specimen (BS 299060) of two taken by them from a small flock has been examined by me and proved to be a first-year individual. Thus, so far as known now, scrub jays of this race are only irregular visitants in that state.

An irregular, partial fall migration to lower elevations apparently occurs in *nevadae* as in *woodhouseii*. This is evidenced by records from Arizona (Breninger, 1901:45; Osgood, 1903:130; Smith, 1908:77; Hargrave, 1932:140), the Virgin River Valley, Utah (Tanner, 1927:198), and Death Valley (200 ft.), California (Grinnell, 1934:68).

Comparisons.—Compared to *grisea* of northwestern Mexico, blue areas of *nevadae* are slightly more purplish; back color is the same; other color differences parallel those between *grisea* and *woodhouseii*. (See p. 30.) In size, *nevadae* is significantly smaller in wing length and larger in bill length; percentage differences between *nevadae* (table 29) and *grisea* (table 33) in these dimensions are as follows: wing length, -6.2; bill length, +16.1.

The important differences between *nevadae* and *superciliosa* of the Sierra Nevada are those which have been described in a comparison of the "*californica*" and "*woodhouseii*" groups of races (p. 208). It may be added that there is a parallelism in the dorsal coloration of *nevadae* and *superciliosa* of western Nevada, but this is not true of the under parts, which contrast strikingly; these differences have been discussed (p. 262). Moreover, my measurements of the two races show greater average differences in certain dimensions than those given by Linsdale (1938:36). Significant differences, expressed in percentage, between *nevadae* and *superciliosa* in northwestern Nevada are as follows (tables 30, 22): wing, +2.4; tail, +2.7; bill length, +13.2; tarsal lengths do not differ significantly. Percentage differences between *nevadae* and *superciliosa* along the east side of the southern Sierra Nevada are as follows (tables 29, 20): wing, +1.8; bill length, +5.8; tail length and tarsal lengths do not differ significantly. Actual interbreeding of the two races is not known to occur in the area considered by Linsdale; if it does occur it is probably sporadic, as in Inyo County to the south. (See p. 261.)

Geographic variation and intergradation.—Characters which separate the restricted race *woodhouseii* from *nevadae* are best seen in comparison of unworn adult specimens representing the eastern and western distributional margins of the two races, respectively. The two races intergrade gradually across a more or less broad belt from western Colorado and central Utah south through northeastern

TABLE 31

MEASUREMENTS OF *A. C. NEVADAE* FROM ARIZONA EXCLUSIVE OF NORTHEASTERN PORTION

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	39	124.7-138.2	130.95±0.49	3.05	2.33
		First-year..	42	121.4-131.7	126.17±0.35	2.26	1.79
	F	Adult.....	29	119.4-129.8	123.97±0.52	2.79	2.25
		First-year..	36	115.5-126.4	121.03±0.39	2.36	1.95
Tail	M	Adult.....	38	137.2-153.1	142.68±0.64	3.98	2.79
		First-year..	41	129.7-143.6	135.56±0.57	3.68	2.71
	F	Adult.....	29	123.8-140.2	132.69±0.73	3.94	2.97
		First-year..	35	119.7-135.3	128.77±0.66	3.89	3.02
Bill length	M	Adult.....	39	17.7- 21.7	19.85±0.15	0.95	4.81
		First-year..	40	17.7- 21.8	19.79±0.15	0.96	4.79
	F	Adult.....	30	17.8- 22.0	19.28±0.21	1.13	5.85
		First-year..	33	16.5- 20.5	18.52±0.17	0.99	5.36
Bill depth	M	Adult.....	38	8.1- 9.4	8.69±0.05	0.34	3.89
		First-year..	40	7.8- 9.2	8.47±0.06	0.36	4.25
	F	Adult.....	29	7.6- 9.1	8.31±0.07	0.38	4.57
		First-year..	34	7.5- 9.1	8.20±0.06	0.36	4.36
Bill width	M	Adult.....	39	7.4- 9.2	8.27±0.07	0.46	5.60
		First-year..	40	7.3- 8.8	7.93±0.05	0.35	4.36
	F	Adult.....	30	7.1- 8.7	7.83±0.07	0.40	5.08
		First-year..	34	7.3- 8.6	7.83±0.06	0.33	4.19
Tarsus	M	Adult.....	38	38.2- 41.7	39.70±0.12	0.76	1.92
		First-year..	41	37.2- 41.0	39.38±0.15	0.95	2.42
	F	Adult.....	29	36.5- 39.8	38.49±0.16	0.85	2.19
		First-year..	36	35.6- 40.3	38.35±0.17	1.01	2.63
Hind toe	M	Adult.....	38	11.5- 13.7	12.48±0.08	0.47	3.76
		First-year..	42	11.5- 13.5	12.32±0.06	0.42	3.40
	F	Adult.....	30	10.0- 12.5	11.93±0.08	0.44	3.71
		First-year..	36	10.5- 12.9	11.95±0.09	0.54	4.51
Middle toe	M	Adult.....	39	17.6- 20.2	18.71±0.10	0.64	3.40
		First-year..	42	17.3- 19.8	18.46±0.08	0.49	2.67
	F	Adult.....	30	16.5- 19.0	17.95±0.11	0.58	3.24
		First-year..	36	17.2- 19.3	18.16±0.08	0.49	2.73
Weights (gm.)	M	6	72 - 80	76.9		

Arizona and western New Mexico. Considerably more fresh material than was available to me is needed before the zone of intergradation can be defined more precisely. For this reason, and also because intergradation is so gradual, the geographic boundary separating *woodhouseii* and *nevadae* is arbitrary and tentative.

Among adult males of *woodhouseii*, color of blue areas is darkest in specimens

from extreme western Oklahoma and northeastern New Mexico. The darkest variant (C 144454, Kenton) is best described as Dark Tyrian Blue—Deep Cadet Blue. In Colorado and most of New Mexico, blue coloration varies slightly, being typically Tyrian Blue—Dark Tyrian Blue, or Tyrian Blue—Cadet Blue. Extremes among New Mexican specimens range from Dark Tyrian Blue—Tyrian Blue (BS 193478, Jicarillo Mountains) to Tyrian Blue (BS 184605, Corona); the latter, although approaching Arizona and Nevada specimens in lightness of coloration, remains more purplish.

In western Colorado, intergradation between *woodhouseii* and *nevadae* is evident in the greater frequency of light variants suggestive of the latter race. Among such variants are two adult males (BS 197390, Meeker; CO 13621, Sedalia), which, however, retain the more purplish tones of *woodhouseii*; two adult females (CO 13619, Sedalia; CO 14064, Douglas County) are comparable to females of the same age from the Great Basin. Occasional variants are as dark-colored, however, as specimens from the eastern range limits of *woodhouseii*; one first-year male (MCZ 91069, Newcastle), although sooty, is of an especially intense coloration among several comparably soiled specimens from the same locality.

Similarly in Utah, occasional specimens comparable to *nevadae* are available from the eastern half of the state (for example, C 122130, 122884, Uinta Basin). The majority of specimens from western Colorado as well as eastern Utah and the Wasatch Mountains are referable to *woodhouseii*, however. To the west, specimens typical of *nevadae* are available from the southwestern part of the state (UU 6490; BS 205725, Washington County). Although other specimens provide additional evidence of intergradation, not enough are available to permit a clear definition of the transition from *woodhouseii* to *nevadae*. All specimens from Nevada are clearly referable to the latter race, however, and the eastern margin of the Great Basin is adopted as a logical line of separation. That line is drawn along the western edge of the Wasatch Mountain axis southward to the Utah-Arizona boundary.

Southward, in northwestern Arizona and southwestern New Mexico, similar evidence of intergradation is seen, but the situation is more indefinite than to the north, for two reasons: first, fresh material permitting clear-cut assignment of specimens to either *nevadae* or *woodhouseii* is scant; second, *nevadae*, best differentiated in the Great Basin and desert ranges of southeastern California, is weakly differentiated in most of Arizona, but is still recognizable on the basis of color characters. To the west of a line cutting across northeastern Arizona, specimens are referable to *nevadae*. Only a few specimens are available to me from northeastern Arizona, but on the basis of evidence from adjoining parts of Utah and New Mexico, that area is tentatively assigned to the range of *woodhouseii*. In southwestern New Mexico, specimens collected along either side of the Río Grande are referable to *woodhouseii*. But to the west intergradation occurs. One first-year female (BS 204503, Florida Mountains) approaches *woodhouseii* in coloration, but others (for example, C 17175, Sierra Hachita; BS 204499, Hidalgo County) are referable to *nevadae*, as are almost all of a large series from immediately adjoining parts of Arizona. Occasional purplish variants, comparable to *woodhouseii*, are seen among specimens from Arizona (AM 20011, Pinal County; MCZ 72609, Fort Prescott), but not from the Great Basin area.

In the Great Basin and the desert ranges of southeastern California, and over a broad belt to the east of the southwestern desert, blue coloration of head and chest becomes lightest and grayest, typically Tyrian Blue—Deep Orient Blue (UU 6490, Pine Valley Mountains; MVZ 28080, Panamint Mountains, the type).

The color differences seen in adults are as clear in first-year birds when specimens from Nevada and southeastern California are compared with others from Colorado and western Oklahoma. The few specimens of this age group from Utah would indicate that variation in the group more or less parallels that of adults and, therefore, is of an intergrading character. In New Mexico and Arizona, however, first-year birds vary to a greater degree than do adults, and a geographic separation such as that proposed on the basis of adults cannot be made. Among first-year males, light variants similar to those from Arizona and clearly referable to *nevadae* (for example, JEL 6252) are lacking in the New Mexican series; conversely, dark variants similar to those from New Mexico and referable to *woodhousei* (for example, MCZ 325917) are lacking in the Arizonan series. But the wide overlap of characters attests to a weaker differentiation of *nevadae* and *woodhousei* in Arizona and New Mexico and to a gradual transition from one to the other, forming a broad, indefinite zone of intergradation.

Over the range of both *woodhousei* and *nevadae* there is a general trend in color of under parts from northeast and north to southwest and south: the gray-brown wash over breast and belly is darker in Colorado and Oklahoma; it is lighter in Arizona. Extremes of this trend are Light Mouse Gray—Mouse Gray (C 144454, Oklahoma) and Smoke Gray (AM 28903, Pinal County, Arizona). Several specimens from south-central and southwestern New Mexico are also light underneath, but the majority of such variants are found in series representing the southern half of Arizona. Due allowance was made here for the possibility that fading might have occurred. I am inclined to regard post-mortem fading in jays kept in dark specimen cases as a negligible factor, since the failure of past workers to differentiate first-year birds from adult birds led them to attribute at least some of the observed differences to fading. I refer now to fresh-plumaged, fall-taken birds, not to more or less worn, sun-faded specimens. The trend here described in *woodhousei-nevadae* is slight and evident in series of specimens only; but that such a trend should exist is not surprising, for the lighter under parts of Arizona scrub jays suggest the neighboring Mexican race *grisea*.

Geographic variation in color of under tail coverts and back parallels that of the head. Geographic differences in back color are detectable in series of specimens only: specimens having brownish backs are most numerous in *woodhousei*; a few approach Hair Brown closely (for example, BS 193476, Manzano Mountains). Such variants are absent in the range of *nevadae*; in the latter race the back is of a duller, more grayish brown, with more or less gray or blue-gray suffusion (for example, BS 259281, AM 28916, UU 6490).

Juvenal specimens have little discernible geographic variation in color that is not obscured by characteristically wide variation among individuals. Lighter coloration in the range of *nevadae*, paralleling the trend seen in adults, is suggested in several individuals from Arizona, Nevada, and the White Mountains of eastern California; in these specimens back coloration falls between Hair Brown and Drab

or approaches the latter color rather closely. The majority of juveniles of *nevadae*, however, are not distinguishable from those of *woodhouseii*. The palest coloration among juveniles of the several North American races of scrub jays is not seen in *woodhouseii* or *nevadae*, as might be expected, but in what is here regarded as typical *superciliosa* in northeastern California.

Three puzzling dark variants from Potosi Mountain, southeastern California, and Nye County, Nevada, are of special interest in that they are similar to dark juveniles collected along the eastern slopes of the Sierra Nevada in Inyo County, California. The backs of these specimens are Mouse Gray, not Hair Brown or lighter. Such dark back coloration is consistent among nonhybrid specimens of *superciliosa* from Inyo County. For lack of a satisfactory series of specimens, no significance can be attached to these observations. But, together with those of *superciliosa* from the eastern slopes of the Sierra Nevada, these suggest that within a restricted area including southern Nevada and adjoining parts of California the tendency is toward dark dorsal coloration in the juvenal plumage. This tendency is best seen in comparisons of specimens from the eastern side of the Sierra Nevada in Inyo County and from the southern San Joaquin Valley.

In northwestern Nevada the range of *nevadae* apparently approaches that of *superciliosa* of the "*californica*" complex closely. Two specimens from Washoe County, both first-year individuals taken in November and May, respectively, were from localities near or within the normal range of *superciliosa*. The two races are not known to interbreed here, however. (See p. 250.) I cannot agree with Linsdale (1938:37) that certain specimens from western Nevada which we have both seen are so nearly intermediate that they can be assigned to one or the other of the two races only with difficulty. "Direct intergradation of a fairly normal kind" does not occur between *superciliosa* and *nevadae*. Their geographic relations are discussed in greater detail under *superciliosa* (p. 261).

Variation in size over the ranges of both *woodhouseii* and *nevadae* is slight. In but one character, length of bill, are the two races differentiated to any significant degree. In the Great Basin (table 30) the bill averages longer than in southern New Mexico and western Texas (table 27). The averages are 21.48 and 19.73 mm., respectively, and $d/\sigma_d = 13.3$. To the north and west, in the Rocky Mountains area (table 26) and Arizona (table 31), bill length does not differ significantly from that found in New Mexico; in this respect, then, scrub jays of Arizona are comparable to those of the Rocky Mountains area. But to north and west, a trend toward *nevadae* is suggested in slight increases in bill length; the differences are not statistically significant, but appear consistently in all age groups. There is no geographic variation in bill depth, but bill width is reduced with increase in bill length in the Great Basin (table 30). Greater width and shorter length of bill along the Mexican border in both *nevadae* and *woodhouseii* represent trends toward neighboring races to the south.

In summary, within the race *woodhouseii* of the A.O.U. Check-list (1981), an east-to-west differentiation in intensity and tone of blue coloration is found most strongly developed in the northeastern and northwestern parts of the range. To a lesser degree, an east-to-west differentiation is evident in color of back. Over the southern parts of the range these color differences are still evident, but weaker.

Dimensions of the bill show a marked increase in length in the Great Basin but not in Arizona. A fairly broad zone of intergradation is suggested between the two differentiates—a zone which becomes more difficult to define to the south in eastern Arizona and western New Mexico.

Several environmental factors offer partial explanation for the north-to-south difference in degree of differentiation between *woodhouseii* and *nevadae*. It may be noted, first, that geographic disposition of mountain ranges and of lowland areas uninhabited by scrub jays undoubtedly influences the paths of dispersal of wandering or migrating individuals. Thus the Wasatch and smaller mountain ranges of central Utah lie in a north-south direction; the lowlands of the Colorado River basin to the east and the deserts and sage flats to the west hinder dispersal or cumulative influences due to population interchange in an east-to-west direction. Contrasting with these geographic features to the south is the east-to-west disposition of the large masses of piñon-juniper woodland and chaparral on the mesas and mountain ranges to either side of the New Mexico-Arizona state line. The latter circumstance would seem to me to allow for a greater interchange of individuals between east and west and thus to explain in part the weaker differentiation of *nevadae* and *woodhouseii* southward.

Another factor affecting degree of differentiation is sheer geographic distance. Thus, northward, the combined range of *nevadae* and *woodhouseii* is approximately 900 miles from east to west; southward, it is approximately 550 miles. Moreover, climatic contrasts between the eastern and western range margins of the combined range are more extreme to the north than to the south (Kincer, 1922, 1928).

Furthermore, it may be noted that on the scattered mountain ranges of the Great Basin the predominant vegetational type occupied by scrub jays is piñon-juniper woodland. To the east and south the area of piñon-juniper is not so great (Shantz and Zon, 1924:8), and other vegetational types inhabited by scrub jays, particularly chaparral dominated by scrub oak, are relatively more extensive. In the Navajo country of northeastern Arizona, for instance, Woodbury and Russell (1945:87) regard the scrub jay as "primarily an inhabitant of oak thickets." This evidence seems to me to bear upon the differences in bill length discussed above. The longer bill of *nevadae* in the Great Basin area suggests the longer, sharper, more highly adapted bill of the piñon jay (*Gymnorhinus cyanocephalus*). Scrub jays, like piñon jays, feed on piñon nuts and in piñon foliage. My present view is that these facts explain fairly adequately the increased bill length of scrub jays in the Great Basin; in all neighboring areas inhabited by them, bill length is shorter and piñon pine either occurs less extensively or is absent. As a matter of fact, *nevadae* has the longest bill, relatively if not absolutely, of all races of the *coerulescens* complex.

The type locality of *woodhouseii* (Baird, 1858:585) is Fort Thorn, ten miles west of Rincon, at 4,500 feet, Doña Ana County, New Mexico (Bailey, 1928:12, 48). This locality falls within the zone of intergradation between *woodhouseii* and *nevadae*. I have not examined the type or any topotypes of the former, but a close study of specimens from south-central New Mexico proves these to be more similar to specimens from south-central Colorado, northeastern New Mexico, and western Oklahoma than to those from Nevada. On the basis of these comparisons the name *woodhouseii* becomes applicable to the eastern differentiate.

Ecologic distribution.—Field studies of scrub jays of the race *nevadae* were made in late May and June of both 1940 and 1942 at a series of stations in the desert ranges of California, including the Argus Range, the Grapevine Mountains, Potosi Mountain, the White Mountains, and Glass Mountain (Mono County). At all these localities the chief habitat of scrub jays was found to be scrubby conifer woodland dominated by piñon (*Pinus cembroides*).

In the Argus Range, May 27–30, 1940, a few jays, apparently representing a single family group, were found in a small grove of piñons at 6,600 feet, south of Mountain Springs Canyon, miles from other piñon areas and surrounded by desert scrub. The group included well-grown juveniles, one of which was collected. It appeared that some members of this group intermittently visited valley-bottom thickets of willow and *Forestiera* around a watering site at 5,500 feet, about a mile from the piñon grove. Single individuals were noted several times in those thickets, and one was observed flying from yucca to yucca along a draw between the piñon grove and valley-floor thickets.

In the Grapevine Mountains the woodland inhabited by scrub jays was fairly dense, piñon being the only tree species except for widely scattered single junipers (*Juniperus utahensis*). Common shrub associates of piñons were *Purshia*, *Ribes*, and *Lycium*. Desert scrub dominated by *Chrysothamnus*, *Artemisia*, *Ephedra*, and *Penstemon* covered open areas and slopes where piñons did not grow, and desert scrub species were mixed with the woodland association. On Potosi Mountain the woodland association was more open, both piñon and juniper being prominent; here the associated shrub species included such striking species as *Arctostaphylos platyphylla*, *Quercus gambelii*, *Q. turbinella*, *Garrya flavescens*, *Ceanothus greggii*, as well as other desert-scrub species. No difference in local abundance of scrub jays was noted between the two areas.

To the north, near Waucoba Mountain, at the southern end of the White Mountains range, piñon-juniper woodland containing shrubs such as *Artemisia*, *Chrysothamnus*, *Purshia*, and *Ribes* is the characteristic plant cover on the west side of the mountains at elevations of 7,000 to 10,000 feet. Scrub jays apparently occur throughout the woodland association. At 7,300 feet, in June, 1942, exceedingly wary family groups were found more or less regularly distributed about a collecting station at the east base of Waucoba Mountain. Along or near Montgomery Creek at the northern end of the White Mountains range, scrub jays were found from 6,900 feet upward in a woodland association differing little from that near Waucoba Mountain. At the former locality, a prominent zone of mountain mahogany occurs at 9,000 to 10,000 feet, between the piñon zone and the higher coniferous forests. Scrub jays occur there as well, but the upper limits of the mountain mahogany more or less mark the upper breeding limits of the jays. Northeast of Glass Mountain, to the west of the White Mountains range, extensive areas of piñon woodland were visited in June, 1942. Here scrub jays were found approximately as common as near Montgomery Creek; at both localities they were somewhat less common than at localities to the south. The piñon woodland of the Glass Mountain area was of rather monotonous character, the common associates of the piñon being *Artemisia*, *Purshia*, *Chrysothamnus*, *Ephedra*, and *Leptodactylon*, except on rough slopes and ridges, where occasional junipers and mountain mahogany were mixed with piñons.

In southern Arizona, where both *Aphelocoma coerulescens* and *A. ultramarina* occur, there is apparently considerable overlap in their vertical distribution; of the two, the scrub jay occurs at higher elevations. In general, the vertical breeding range of *A. ultramarina* is 4,500–6,500 feet; that of *A. coerulescens*, 5,000–7,500 feet. *A. ultramarina* is an associate of evergreen oaks (Scott, 1886:81); *A. coerulescens* is characteristic of chaparral-covered, rough mountain slopes on which scrub oaks and mountain mahogany are prominent (Swarth, 1904:29; Wetmore, 1921:60). Throughout its breeding range generally, *A. c. nevadae* occurs characteristically either in piñon-juniper woodlands (Anthony, 1892:364; Fisher, 1903:35; Swarth, 1924:186), chaparral areas (van Rossem, 1936:34), or mixtures of the two vegetation types forming a scrub woodland.

A post-breeding dispersal of scrub jays to higher elevations has been observed on some of the larger mountain ranges. On the Charleston Mountains, van Rossem (*ibid.*) noted jays in late July and August above the normal vertical range of 6,000–7,000 feet, at elevations of 9,000 feet near the upper limits of piñon and mountain mahogany and of 10,000 feet in coniferous forests where scrub jays were recorded several times in association with Steller jays. Scrub jays were also observed by van Rossem on Sheep Mountain in September at 9,000 feet in yellow pines. In southern Arizona, Bailey (1923:33) recorded them in winter in oak groves at elevations below the breeding range; Scott (1887:20) reports that in that season they may associate with *A. ultramarina*.

Aphelocoma coerulescens texana

Racial characters.—Compared with *woodhouseii*, blue areas slightly darker; pileum, hind neck, sides of head and neck Deep Cadet Blue—Dark Tyrian Blue; feathers of lower throat and upper chest edged with slightly darker blue, the collar pattern thus appearing more contrasting; collar band reduced somewhat, however, the average amount of blue on the middle of the chest being less than in *woodhouseii*; lower breast suffused with dull grayish brown (Mouse Gray—Drab Gray), thus less grayish than *woodhouseii*; belly lighter (Smoke Gray—Light Mouse Gray), the whitish area about anus larger; under tail coverts white, the longest feathers tinged with pallid blue in approximately 75 per cent of adult males; back darker (Hair Brown or Hair Brown—Fuscous), suffused consistently but only slightly with blue. Bill heavier, less pointed, similar to *woodhouseii* in other dimensions; percentage differences between adult males of *woodhouseii* (table 26) and *texana* (table 32) are as follows: bill depth, +8.6 per cent; bill width, +6.3 per cent. Wing-tail ratio, 0.908:1. (See table 32 for other statistical data.)

Juvenal plumage differs from *woodhouseii* in that under parts are lighter; throat and lower breast whiter; belly and under tail coverts white or whitish; upper breast less gray, more brown (Drab—Mouse Gray in darkest parts); collar reduced to indistinct, broad band; upper parts similar or slightly browner than in *woodhouseii*.

Geographic distribution.—Regions of the southern Concho River drainage and the Edwards Plateau in west-central Texas, from Tom Green and Concho counties south to Kerr, Edwards, and Crockett counties.

According to Oberholser (1920:91), scrub jays occur north to Taylor County. Reports of this form from extreme western Texas under the name *texana* are referable to the race *woodhouseii*.

Comparisons.—Compared with *cyanotis* of eastern Mexico, the blue areas of *texana* are darker and more purplish; the back is darker and less suffused with blue; the collar pattern is slightly more pronounced (more blue); under parts

TABLE 32
MEASUREMENTS OF A. C. TEXANA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	47	125.3-136.9	130.17±0.41	2.82	2.16
		First-year..	19	122.9-132.3	125.95±0.59	2.57	2.04
	F	Adult.....	37	119.5-128.1	123.51±0.35	2.13	1.72
		First-year..	8	117.9-124.9	121.12		
Tail	M	Adult.....	47	134.0-152.1	143.36±0.60	4.10	2.85
		First-year..	19	133.3-144.2	136.74±0.71	3.11	2.28
	F	Adult.....	37	125.5-140.4	132.73±0.49	2.96	2.23
		First-year..	8	124.6-134.1	129.63		
Bill length	M	Adult.....	47	17.6- 22.0	19.57±0.14	0.98	5.03
		First-year..	17	17.4- 20.5	19.48±0.22	0.90	4.60
	F	Adult.....	37	17.1- 20.3	18.60±0.13	0.82	4.42
		First-year..	10	18.0- 19.4	18.85		
Bill depth	M	Adult.....	47	8.6- 10.1	9.31±0.05	0.35	3.86
		First-year..	17	8.3- 9.8	9.14±0.10	0.42	4.57
	F	Adult.....	36	8.0- 9.5	8.71±0.06	0.37	4.20
		First-year..	9	8.3- 9.6	8.72		
Bill width	M	Adult.....	46	7.8- 9.8	8.73±0.07	0.45	5.11
		First-year..	17	7.8- 9.0	8.39±0.09	0.38	4.49
	F	Adult.....	38	7.2- 9.2	8.41±0.06	0.40	4.75
		First-year..	10	8.2- 9.6	8.65		
Tarsus	M	Adult.....	44	37.4- 43.1	39.83±0.18	1.17	2.94
		First-year..	18	38.1- 42.2	39.70±0.22	0.92	2.32
	F	Adult.....	38	36.6- 41.4	38.77±0.18	1.08	2.79
		First-year..	10	37.1- 40.2	38.63		
Hind toe	M	Adult.....	47	11.7- 13.8	12.97±0.06	0.42	3.24
		First-year..	19	12.1- 13.9	12.97±0.11	0.50	3.86
	F	Adult.....	38	11.3- 13.6	12.63±0.09	0.53	4.20
		First-year..	11	11.7- 13.5	12.61		
Middle toe	M	Adult.....	46	17.7- 20.9	18.99±0.10	0.66	3.47
		First-year..	19	18.3- 20.5	19.36±0.14	0.60	3.09
	F	Adult.....	36	17.3- 19.6	18.50±0.09	0.54	2.92
		First-year..	10	17.5- 19.6	18.64		

washed with more Smoke Gray; the under tail coverts are more frequently tinged with blue. In size, *texana* (table 32) differs from *cyanotis* (table 34) primarily in having a shorter wing and longer bill; the differences, expressed in percentage, are as follows: wing, - 6.8; bill length, + 4.9.

Intergradation.—Evidence of intergradation westward between *texana* and *woodhouseii* is scant. An ecologic gap, the arid *Larrea-Agave* desert of the Pecos Valley (Bailey, 1905:25), apparently separates the two races, but interchange

between them is probable. Blue coloration of a first-year female (BS 184177) taken in western Crockett County, near the Pecos River, on August 7, 1902, is light, suggesting that of *woodhousei*, but in other respects it is comparable to *texana*. The under tail coverts of one summer-taken adult male (BS 184455) from Edwards County are exceptionally dark, suggesting *woodhousei*, although in all other characters it represents *texana*. These two specimens might be thought to represent extreme variants within *texana*, but both are distinctive enough to be regarded as evidence of sporadic interbreeding between the two races.

TABLE 33
MEASUREMENTS OF ADULTS OF A. C. GRISEA

	Sex	No. of specimens	Range	Mean
Wing	M	7	133.6-145.0	138.61
	F	6	130.2-135.6	133.30
Tail	M	7	143.4-151.0	146.51
	F	6	130.4-139.2	136.67
Bill length	M	7	17.4- 19.5	18.46
	F	6	16.8- 19.3	18.00
Bill depth	M	7	8.3- 9.2	8.64
	F	6	8.0- 8.7	8.38
Bill width	M	7	7.6- 8.9	8.26
	F	6	8.1- 8.8	8.35
Tarsus	M	7	38.4- 42.3	40.63
	F	6	37.6- 39.1	38.50
Hind toe	M	7	11.8- 13.3	12.64
	F	6	11.6- 12.8	12.20
Middle toe	M	7	17.8- 20.0	18.97
	F	6	17.6- 18.6	18.15

Evidence of intergradation of *woodhousei* with *texana* in extreme western Texas has been discussed. (See p. 285.)

Ecologic distribution.—Scrub jays of the race *texana* characteristically inhabit oak and conifer thickets covering irregular slopes and filling short draws and the upper ends of most valleys in the rough, hilly country of west-central Texas (Lacey, 1903:151; Smith, 1916:190, 1918:212). Several species of oaks (*Quercus*) (Bray, 1906:78) are important as major components of scrub communities and as sources of fall and winter food for scrub jays. Conifers with which these jays are here associated are junipers (*Juniperus sabinoides*). Streamside thickets are also frequented, especially in dry weather (Smith, 1916:190, 1918:212). Nests are placed 4 to 6 feet above the ground (Lacey, 1903:151).

No other species of jay breeds in this portion of Texas, but *Cyanocitta cristata*

apparently occurs as an infrequent fall or winter visitant (Lloyd, 1887:289; Lacey, 1911:211).

Aphelocoma coerulescens grisea

Racial characters.—Compared to *woodhousei*, lighter in coloration throughout; pileum, hind neck, and sides of head, neck, and chest lighter and less purplish (Deep Orient Blue—Chapman's Blue); back lighter (Hair Brown—Drab), suffused with dull blue; throat streaked with lighter gray; blue of collar pattern reduced on upper mid-breast; middle and sides of breast lighter, washed with dull brownish gray (Smoke Gray—Mouse Gray); belly lighter, becoming white in anal area; under tail coverts white. Wings longer and bill shorter, heavier basally; percentage differences in adult males are as follows: wing, +5.9; tail, +1.8; bill length, -7.4; bill width, +1.7; tarsus, +2.3. Wing-tail ratio, 0.946:1. (See table 33 for other statistical data.)

Geographic distribution.—Sierra Madre of northwestern Mexico, from northern Durango (Cerro Prieto and La Boquilla) north to central Chihuahua (Bustillos). (See fig. 10.)

Little is known of the distribution of this race. Papers by Nelson (1899b) and W. DeW. Miller (1906) are the only ones known to me which offer original data. Northward, along the main axis of the Sierra Madre, there is presumably no major break in the distribution of scrub jays, and *grisea*, intergrading with *nevadae*, may extend farther north than here stated. Southward, it is probable that *grisea* ranges somewhat farther than indicated.

A puzzling problem is the apparent absence of scrub jays from southern Durango, Zacatecas, Jalisco, and Michoacán. From what is known of the general physiographic and vegetational features of western Mexico, a distribution comparable to that of *Aphelocoma ultramarina* and *Cyanocitta stelleri* might be expected. Future field investigations may lead to the discovery of scrub jays in southern Durango, Zacatecas, and Jalisco.² Michoacán, however, has received more attention from field naturalists and collectors; that scrub jays are absent from at least the west-central part of that state seems rather definitely established (not reported by Blake and Hanson, 1942).

Comparisons.—The race *grisea* is not so closely similar to *woodhousei* (Nelson, 1899:27) or *texana* (Ridgway, 1904:331; Hellmayr, 1934:54) as it is to *cyanotis*. On the basis of the limited material available, I would suggest that *grisea* be best regarded as one of the comparatively weakly marked races of the *coerulescens* complex, approximately comparable in degree of differentiation to *cactophila* or *oocleptica*. For comparisons of *grisea* and *cyanotis*, see page 305; of *grisea* and *nevadae*, page 291.

Variation and intergradation.—On the basis of limited material it appears that age variation in *grisea* is comparable to that of most races of *coerulescens*. Under tail coverts are typically white, in first-year males at least (AM 92301, Las Bocas, Durango), but the longest under tail coverts may be tinged with pallid blue.

Intergradation with *nevadae* and *woodhousei* is shown in specimens from central Chihuahua, the under parts of which are washed with more gray; but these are assignable to *grisea* on the basis of light coloration of belly and white under tail coverts. Intergradation between *grisea* and the two more northern races prob-

² I have been informed recently by B. T. Moore that there are several specimens of *grisea* in his collection from the Chihuahua-Durango area, including some from southern Durango. Additional specimens from even farther south, from Jalisco, may belong to this form.

TABLE 34

MEASUREMENTS OF A. C. CYANOTIS FROM SAN LUIS POTOSÍ, HIDALGO, AND MÉXICO

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult	29	134 4-144.5	130.72±0.42	2.20	1.64
		First-year..	14	129 6-138 5	134.29		
	F	Adult	15	131 0-137 9	134.13		
		First-year..	4	124 3-132.4	129.75		
Tail	M	Adult	28	136.6-151.7	143.46±0.72	3 83	2.68
		First-year..	14	130 6-140.5	136 00		
	F	Adult	14	130.1-144 5	136.93		
		First-year..	4	125.9-139.5	130 50		
Bill length	M	Adult	30	16.6- 21.1	18.65±0.19	1.03	5.51
		First-year..	13	17.5- 20.5	18.54		
	F	Adult	15	16.1- 19.3	17.88		
		First-year..	4	16.4- 17.7	17.05		
Bill depth	M	Adult	30	8.4- 9.6	9.12±0.06	0.33	3.66
		First-year..	13	8.5- 9.4	8.97		
	F	Adult	13	8.1- 9.6	9.08		
		First-year..	4	8.6- 9.7	9.05		
Bill width	M	Adult	29	7.5- 9.7	8.55±0.10	0.51	6.01
		First-year..	13	7.4- 9.1	8.37		
	F	Adult	15	7.6- 9.2	8.44		
		First-year..	4	8.3- 8.9	8.50		
Tarsus	M	Adult	30	37.5- 42.4	40.20±0.19	1.06	2.64
		First-year..	14	38.8- 41.7	40.01		
	F	Adult	14	37.0- 40.7	39.67		
		First-year..	4	38.5- 41.2	39.90		
Hind toe	M	Adult	30	11.9- 13.6	12.54±0.08	0.45	3.59
		First-year..	13	11.6- 13.8	12.59		
	F	Adult	15	11.5- 13.6	12.46		
		First-year..	4	12.4- 12.8	12.65		
Middle toe	M	Adult	27	17.2- 20.0	18.86±0.15	0.79	4.21
		First-year..	13	18.2- 20.2	19.19		
	F	Adult	14	17.3- 20.1	18.72		
		First-year..	4	18.1- 19.4	18.63		

ably occurs over northwestern Chihuahua and northeastern Sonora; I have seen no specimens from either of these areas.

So far as known, *grisea* does not intergrade with *cyanotis*.

Ecologic distribution.—According to Nelson (1899b:27), *grisea* occurs in the "oak woods" of the Sierra Madre; but according to information which E. A. Goldman sent to R. T. Moore (letter, September 19, 1950), *grisea* occurs in the piñon pine belt on the east slope of the Sierra Madre.

Aphelocoma coerulescens cyanotis

Racial characters.—Compared with *woodhouseii*, blue areas generally duller (less purplish); pileum, hind neck, and sides of head and neck less purplish (Tyrian Blue—Chapman's Blue); back Hair Brown, suffused variably, sometimes heavily, with dull blue; superciliary line obsolescent, not extending back above auricular region as in *woodhouseii*; under parts lighter; throat streaked with lighter gray; feathers of upper chest, including sides, edged laterally with light grayish blue, which may be much reduced and replaced by dull gray; mid-chest, including sides, washed with Smoke Gray, becoming white on lower belly; under tail coverts white, occasionally tinged with dull grayish blue. Wing longer; bill shorter, but heavier basally; percentage differences in adult males are as follows (tables 26, 34): wing, +6.7; bill length, -6.4; bill depth, +6.4; bill width, +5.3. Wing-tail ratio, 0.974:1. (See table 34 for other statistical data.)

Juvenal plumage: only one specimen seen (LCS 15666, Ypiña); differs from *woodhouseii* in having lighter under parts, almost white belly, and darker, browner upper parts; similar to *texana* in having dull brownish-gray wash over upper chest and lower throat; apparently browner than any examples of *texana* on upper chest and dorsally as well.

The brief characterization of *cyanotis* given in Ridgway's monograph (1904:335) is approximately correct. Two characters emphasized in his original description (1887:357) are both without basis: the back is "strongly tinged with blue" only in occasional variants; sides of the head are not "uniform bright blue, like crown," but blackish with a blue overcast as in virtually all races of *coerulescens*. Thus the vernacular names "blue-eared jay" and "blue-cheeked jay" are misnomers and should be dropped.

Individual variation.—Blue coloration within *cyanotis*, as now understood, appears to be more than usually variable, approaching *superciliosa* of the "*californica*" group in this respect. This is of particular interest in conjunction with the characters displayed by intergrading populations between *cyanotis* and *woodhouseii* and *texana* to the north. Dark variants of *cyanotis* approach *woodhouseii* closely; although never so purplish as typical representatives of the latter, they are best described in terms of the same colors, namely, Dark Tyrian Blue—Deep Cadet Blue (LCS 15668, Ypiña). Lighter variants approach Tyrian Blue—Chapman's Blue (C 108087, Ypiña). The majority of fresh-plumaged specimens I have seen are closer to the latter extreme.

Variation of the same order is seen in the amount of blue in the collar pattern of adult males. About half of them lack blue edging on feathers of the mid-chest, the blue being replaced by dull brownish gray. The remaining specimens show variable amounts of dull grayish-blue edging; the specimen most strongly colored in this respect (MCZ 98797, Ypiña) is lighter and duller than typical *woodhouseii*.

Among adult males, under tail coverts of seven out of twenty-four specimens, or 24 per cent, are tinged terminally with blue or gray blue (Light Columbian Blue or close to that shade).

One adult male (BS 144758, Jesús María) is a notable exception among all other specimens of *cyanotis*. It is unusually blue throughout. The head color is similar to that of *woodhouseii* (Dark Tyrian Blue—Deep Cadet Blue) and richer than that of any other specimen of *cyanotis*; the throat and collar pattern is comparable to that of the most richly colored specimens of *woodhouseii*. Unlike any other specimen of *coerulescens* I have seen, the back is of a strong blue color (Tyrian Blue). The under tail coverts, however, are mostly white, and only the longest ones are tinged slightly with light blue.

Among first-year males, blue areas average duller than in adults; they appear

TABLE 35

MEASUREMENTS OF *A. C. CYANOTIS* FROM SOUTHERN COAHUILA

	Sex	Age group	No. of specimens	Range	Mean
Wing	M	Adult.....	7	130.0-135.3	133.29
		First-year.....	3	126.4-133.5	
	F	Adult.....	1	131.3	
		First-year.....	2	125.6-126.1	
Tail	M	Adult.....	6	136.4-151.4	140.17
		First-year.....	3	130.8-138.3	
	F	Adult.....	2	131.1-138.1	
		First-year.....	2	124.4-130.0	
Bill length	M	Adult.....	7	18.0- 21.9	20.07
		First-year.....	3	18.5- 19.5	
	F	Adult.....	2	18.8- 19.1	
		First-year.....	2	17.2- 17.7	
Bill depth	M	Adult.....	5	8.9- 9.3	9.09
		First-year.....	3	9.0- 9.5	
	F	Adult.....	2	8.7- 8.9	
		First-year.....	2	8.8	
Bill width	M	Adult.....	7	8.5- 9.3	8.79
		First-year.....	3	8.4- 8.6	
	F	Adult.....	2	8.3- 8.6	
		First-year.....	2	8.7- 9.3	
Tarsus	M	Adult.....	7	40.0- 42.4	41.01
		First-year.....	2	40.8- 41.3	
	F	Adult.....	2	38.5- 38.9	
		First-year.....	2	38.9- 40.2	
Hind toe	M	Adult.....	7	12.0- 13.7	12.97
		First-year.....	3	12.6- 14.1	
	F	Adult.....	2	12.2- 12.7	
		First-year.....	2	12.2- 12.5	
Middle toe	M	Adult.....	7	18.5- 20.6	19.39
		First-year.....	3	19.2- 21.1	
	F	Adult.....	2	18.8- 18.9	
		First-year.....	2	18.4- 19.1	

to vary in the same degree. In the limited series I examined, none approaches the most strongly colored adult males (excluding BS 144758). Quantity of blue in the collar varies as in adults, the most strongly colored individual (MCZ 98812) being comparable in this respect to the extreme among adult males. Under tail coverts of five out of twelve specimens are tinged lightly with pale blue or gray blue.

Available specimens of females are too few for an elaboration of this intraracial analysis. In first-year females the collar pattern may be much reduced and without blue laterally as well as medially (MCZ 98803).

Geographic distribution.—Mountain ranges of east-central Mexico from southern Coahuila (Saltillo) south to the states of México (Tlalpan, D.F.) and Hidalgo (Real del Monte).

Cyanotis probably ranges farther north into Coahuila than stated above; there it may be found intergrading with *woodhouseii*, as is true to a certain extent in southern Coahuila. (See below.) As shown by Oberholser (1917:94), *cyanotis* does not occur north of the Mexican border. Use of this name for specimens from southwestern Texas (Fisher, 1894:327; Bendire, 1895:382; Ridgway, 1904:337, etc.) is erroneous; they should be either *texana* or *woodhouseii*. (See discussion, p. 403.) Records of *cyanotis* from Durango (A.O.U. Check-list Committee, 1902:321; Ridgway, 1904:335) are also in error; these apply to *grisea* (Miller, 1906:170).

Southward, *cyanotis* probably does not range beyond the southeastern borders of México and Hidalgo. Ridgway (1904:335) assigns Stone's (1890:214) records of "*Aphelocoma sumichrasti*" from mounts Ixtaceihuatl and Popocatepetl to *cyanotis*; but I would expect specimens from these localities to be intergrades between the two races.

It is possible that scrub jays of this race will be found in northeastern parts of Zacatecas and Guanajuato and in Querétaro; I find no records for any of these states.

Comparisons.—For comparison of *cyanotis* and *texana* see page 298.

Compared with *grisea* of Durango and Chihuahua, *cyanotis* is slightly darker (less grayish) dorsally; in collar markings and color of under parts, the two races are similar. In size, the two do not appear to differ significantly in any dimensions; data for *grisea* are inadequate for statistical comparisons. Bill proportions are similar in the two races, but the bill of typical *cyanotis* (table 34) is larger in all dimensions; the combined slight differences in length, depth, and width produce a detectable total difference which may prove to be one of the chief differences in size between the two races. The bill of *cyanotis* in Coahuila (table 35) is conspicuously larger than that of *grisea*; *cyanotis* from Coahuila appears to differ further from *grisea* in having slightly shorter wings and tail.

Compared with *sumichrasti* to the south, blue areas of *cyanotis* are more purplish but slightly duller; the back is characteristically suffused with blue, whereas in *sumichrasti* the back is without blue; the collar pattern is more pronounced in *cyanotis*; the middle and lower breast are washed with more Smoke Gray. *Cyanotis* is smaller than *sumichrasti* in all dimensions; percentage differences are as follows: wing, -2.9; tail, -2.3; bill length, -2.4; tarsus, -4.2.

Geographic variation and intergradation.—Specimens from Coahuila are darker underneath than those here regarded as typical *cyanotis* from southwestern San Luis Potosí. Also, under tail coverts are tinged more frequently among the Coahuilan specimens, of which five out of seven males in good plumage show tinged coverts. These differences represent intergradation northwardly with *woodhouseii*.

In other characteristics the specimens from Coahuila are puzzling. As further evidence of intergradation with *woodhouseii*, the dorsal coloration is slightly darker than in typical *cyanotis* (BS 144749, Carneros); but two specimens, a first-year male (C 122980) and a first-year female (C 122907), both taken on Diamante Pass, are generally darker than either *cyanotis* or *woodhouseii* of western Texas.

In size characters, Coahuila specimens (table 35) are intermediate in wing length between *woodhouseii* of western Texas and southern New Mexico (table 27) and typical *cyanotis* (table 34). Specimens from Coahuila are too few for valid comparisons, but certain suggestive points may be noted. The bill is heavy basally, like that of typical *cyanotis*, but is as long as that of *woodhouseii*. It would appear also that the feet of Coahuilan specimens are as large as those of typical *cyanotis*, if not larger.

Thus, in most characters, scrub jays from Coahuila show intergradation between *woodhouseii* and *cyanotis*. On the basis of the relatively large difference in wing length and darker coloration, however, it may prove advisable, after adequate material is acquired, to recognize the Coahuilan population as a separate race. For the time being, however, they are to be referred to *cyanotis*, although atypical.

Southward, *cyanotis* intergrades with *sumichrasti* in the region along the borders between Hidalgo and México, and between Morelos and Puebla. Evidence of such intergradation is scant, however; one specimen from Hidalgo (BS 144733, Tula), although worn, is seen to have less blue on the middle and the sides of the chest when compared with similarly worn specimens of *cyanotis*. In this respect it suggests the race *sumichrasti*. In size, two specimens from Hidalgo fall into the range of overlap between *cyanotis* and *sumichrasti* for most dimensions.

Two specimens from the Federal District (BS 144754, Tlalpan; MVZ 93595, Santa Rosa) suggest intergradation with *sumichrasti* in that the bodies of both are as dark (Hair Brown—Fuscous) as the darkest variants of typical *cyanotis*. The blue suffusion is reduced, but not more so than in normal variants of typical *cyanotis*. In dimensions, only the tarsal lengths suggest *sumichrasti* in that both closely approach the upper limits of variation. Thus, evidence of intergradation with *sumichrasti* is weak.

Ecologic distribution.—In San Luis Potosí, scrub jays occur in open, sparsely vegetated areas characterized by live oaks, at elevations of 7,000 to 8,000 feet (Jouy, 1894:782). In southeastern Coahuila, Sutton and Burleigh (1939a:23, 35) found scrub jays at 7,800 feet in an association of juniper, low-growing oak, scrub pine, and tall fir. Other avian species present included bush tits (*Psaltiriparus minimus*), juncos (*Junco phaeonotus*), and chickadees (*Parus sclateri*). Burleigh and Lowery (1942:185, 196), dealing with the same area, stated that scrub jays are found primarily on mountain slopes below 7,800 feet down to 5,300 feet. Farther south, scrub jays occur at higher elevations; Stone (1890:214) reports them as ranging "up to 11,000 ft." on mounts Ixtaccihuatl and Popocatepetl. Brief reports (Jouy, 1894:782) of small, late autumnal flocks of scrub jays of the race *cyanotis*, of their feeding on the ground, and of their preference for acorns suggest that habits of that race closely resemble those of Californian races.

THE "SUMICHRASTI" GROUP OF RACES

Aphelocoma coerulescens sumichrasti

Description and racial characters. Male: adult fall plumage.—Upper parts: pileum, hind neck, and sides of neck Cadet Blue—Tyrian Blue; auricular region velvety black; subauricular and suborbital regions brownish black washed with dull blue; lores black; superciliary line white, irregular, lacking anteriorly, extending from above eye to auricular patch; back grayish brown

(Hair Brown—Fuscous) with very little or, usually, no blue suffusion; scapulars and rump grayish blue (approaching Delft Blue—Deep Dutch Blue); upper tail coverts Columbian Blue.

Under parts: chin, throat, and mid-chest white streaked with pale gray; sides of chest dull grayish brown (Hair Brown); mid-chest slightly lighter, with light-gray or gray-blue lateral edging of feathers forming an obscure collar; blue edging increased and brighter laterally, but not produced into a blue wedge on each side of upper chest, as seen in all other races of *coerulescens* except *remota*; mid-chest with faint brownish-gray wash; remainder of under parts white; ankle feathers Smoke Gray.

Wings and tail: remiges and feathers of alula dark grayish blue (Deep Orient Blue—Tyrian Blue); coverts and innermost secondaries slightly brighter than remiges; wing coloration otherwise similar to that of *woodhouseii*; rectrices similar to remiges or slightly duller and darker (Dark Tyrian Blue—Deep Orient Blue). Wing-tail ratio, 0.980:1. (See table 36 for other statistical data.)

Bill: black, moderately heavy; hook present, short; culmen more or less sharply curved terminally.

Feet and iris as in *woodhouseii*.

The series of *sumichrasti* available to me is too small and contains too few fresh-plumaged specimens to permit description of differences between adult and first-year birds of each sex; presumably these differences are comparable to those of other races of *coerulescens*.

Male and female: juvenal plumage.—Upper parts: pileum, hind neck, sides of head, neck, and upper chest, and upper tail coverts dark grayish brown (Fuscous—Hair Brown); back, scapulars, and wing coverts similar or slightly lighter; pileum tinged with dull blue; superciliary line short and much reduced, consisting of faint streaks above and behind eye.

Under parts: chin and throat dull white; sides of throat and sides and middle of chest grayish brown (Drab—Light Drab), dull white of throat extending over upper mid-chest as broad axial streaks; lower breast also washed with grayish brown, but lighter; belly and anal area white; under tail coverts whitish or pale brownish gray; ankle feathers darker (Mouse Gray).

Wings and tail: remiges dark dull blue (Tyrian Blue—Deep Delft Blue), slightly darker and brighter than in *woodhouseii*, otherwise wing coloration similar to that race; rectrices similar to remiges or slightly darker (Dark Tyrian Blue—Deep Delft Blue).

Bill and feet as in *woodhouseii*.

Geographic distribution.—Southeastern portion of the Mexican plateau, from Tlaxcala (Huamantla) and west-central Veracruz (Perote) south through Puebla into Oaxaca (Tlapancingo, Ejutla, Mount Zempoaltepec); northwardly, in Veracruz, Puebla, and México, apparently confined to high mountains at elevations of 9,000 to 10,500 feet (Stone, 1890:214; Davis, 1945:279).

A. c. sumichrasti represents the southeasternmost Mexican race of the scrub jay. The species thus does not cross the Isthmus of Tehuantepec as does *A. unicolor*; on the other hand, *A. coerulescens* ranges south along a mountain chain connecting the Sierra Madre Oriental south of Puebla with the Sierra Madre del Sur and occurs along the latter range, whereas *A. ultramarina*, in this part of Mexico, is confined to the former range.

Comparisons.—Differences separating the race *sumichrasti* from members of the “*woodhouseii*” group have been discussed (p. 208). For a comparison of *sumichrasti* and *cyanotis* see page 305.

In linking the Mexican forms of *coerulescens* with those of California under the specific name *californica*, Oberholser (1918c:166) stated that “some individuals of . . . *sumichrasti*, however, are difficult, if not impossible, certainly to distinguish from *immanis* or *hypoleuca*.” I find these races easily separable on the basis of color as well as size. *Sumichrasti*, although suggesting the “*californica*” group of races

TABLE 36
MEASUREMENTS OF A. C. SUMICHRISTI

	Sex	Age group	No. of specimens	Range	Mean
Wing	M	Adult.....	8	140.0-149.8	143.87
		First-year ...	7	137.0-141.9	140.14
	F	Adult....	5	134.6-139.4	136.60
		First-year.....	3	130.1-133.9	
Tail	M	Adult... ..	8	139.0-152.6	146.88
		First-year.....	6	139.5-150.1	143.17
	F	Adult.....	5	135.2-142.8	139.20
		First-year.....	2	135.6-138.3	
Bill length	M	Adult.....	8	17.6- 19.9	19.11
		First-year.....	3	16.9- 18.8	
	F	Adult.....	5	17.3- 18.9	18.16
		First-year.....	2	16.3- 19.0	
Bill depth	M	Adult.....	8	9.0- 10.1	9.65
		First-year.....	3	8.9- 9.2	
	F	Adult.....	5	8.4- 9.4	8.87
		First-year.....	1	9.6	
Bill width	M	Adult.....	8	8.6- 9.9	9.00
		First-year.....	3	8.7- 8.9	
	F	Adult.....	5	7.9- 9.0	8.41
		First-year.....	2	8.7- 8.8	
Tarsus	M	Adult.....	8	40.5- 44.2	41.96
		First-year.....	7	40.4- 42.9	41.23
	F	Adult.....	5	39.0- 39.7	39.96
		First-year.....	2	39.9- 40.7	
Hind toe	M	Adult.....	8	12.8- 14.5	13.44
		First-year.....	7	12.2- 14.1	13.27
	F	Adult.....	5	12.4- 13.9	13.16
		First-year.....	3	12.4- 13.5	
Middle toe	M	Adult.....	8	19.3- 21.1	20.16
		First-year.....	7	18.4- 20.6	19.47
	F	Adult.....	4	18.7- 20.3	19.68
		First-year.....	3	18.6- 20.1	
Weights (gm.)	M	5	93 -108	100.2
	F	6	93 -103	94.9

in certain characters, is nevertheless more closely related to the "*woodhousei*" group.

Variation and intergradation.—Available material is inadequate for a discussion of geographic variation. Under tail coverts of one adult male (PAC 25362, Chalchicomula) are tinged with blue; even though usually white, as in *cyanotis*, under

tail coverts may be tinged in both races, but apparently this occurs less frequently, if not rarely, in *sumichrasti*.

Sumichrasti intergrades northwardly with *cyanotis* (see p. 306) and westwardly, presumably, with *remota*, but its geographical relationships with the latter race remain unknown.

Ecologic distribution.—Little is known of the habitat of scrub jays of this race. They have been reported from the lower elevations of mountain pine forests (Stone, 1890:214), from rough, scrub-covered hill country (Sutton and Burleigh, 1942:419), and from broken juniper-pine areas west of Cofre de Perote (Davis, 1945:279).*

Aphelocoma coerulescens remota

Racial characters.—Compared with *sumichrasti*, coloration duller and lighter; pileum, hind neck, and sides of neck slightly duller (Chapman Blue—Tyrian Blue); back lighter and more grayish (Hair Brown), suffused with dull blue; superciliary line obsolescent, less developed than in *sumichrasti*; collar pattern reduced to light-gray edging on feathers of upper chest, a reduction which represents an extreme in *coerulescens* complex; sides of upper chest Hair Brown with little or no blue; under parts otherwise similar to those of *sumichrasti*. In size, larger than *sumichrasti*; percentage differences in adult males are as follows: wing, +1.2; tail, +1.8; bill length, +4.0; tarsus, +1.1. Wing-tail ratio, 0.974:1. (For other statistical data see table 37.)

Juvenal plumage generally similar to *sumichrasti*; back similar or slightly grayer; upper chest similar or slightly darker.

This characterization differs in certain important respects from that given by Griscom (1934:392). The blue of *remota* is slightly lighter than that of *sumichrasti*, as noted by Griscom, but the difference is no stronger than that between *texana* and *cyanotis* or *cyanotis* and *sumichrasti*, all of which are stated by Griscom to be "dull azure." The unique character of light shaft streaks on the back, attributed by Griscom to *remota*, is, as suggested indirectly by Berlioz (1937:175), based on worn specimens; similar shaft streaks are to be seen on worn specimens of other races. The brownish or "velvety" black of loreal, orbital, and auricular regions is not unique in *remota*, but is identical with that of *sumichrasti*. Thus *remota* exhibits no "unique" characters. All characters distinguishing this recognizable race are relative, and among them the most striking is the reduction of the collar pattern, in which respect *remota* represents an extreme.

Geographic distribution.—Sierra Madre del Sur in the state of Guerrero. This race is known chiefly from the region about Chilpancingo. Recently Berlioz (1937:174) has reported *remota* from Apetlanca, some distance northwest of Chilpancingo; but his report needs confirmation, for that locality appears to be at an ele-

* *A. o. sumichrasti* was observed and collected, March 24 and April 24–26, 1950, in central Oaxaca. The habitats were scrub woodland (Matatlán, 27 mi. SE Oaxaca, 5,600 ft.), palmetto scrub (18 mi. S Petalcingo, 5,000 ft.), open thorn forest near upper limits of the tropical deciduous forest (2 mi. S Petalcingo, 4,600 ft.), and, most commonly, edges and openings of pine-oak forest (Yalina, Ixtlán, and 4 mi. SE Cerro San Felipe, 5,000–9,000 ft.). It would appear that increased length of wing and tail in the southern Mexican races (*sumichrasti* and *remota*) is an adaptation to a combination of conditions arising from character of vegetation and rugged physiography. Generally, trees are not only taller, larger, and more open than those available to scrub jays in California, but frequent steep slopes introduce a considerable vertical component into the normal flight range. Compared to more northern races, *sumichrasti* gives the impression of a relatively large bird. It is clearly superior to Californian races in flight speed and maneuverability. *A. o. sumichrasti* was observed to fly upslope directly and rapidly, without the labor evident in less steep flights of *californica* or *occidentalis*. Otherwise, in call notes or behavior, no important differences were detected between *sumichrasti* and Californian scrub jays. While these observations were brief, it may be said, in their defense, that extensive field experience with the northern races alerts one to features of behavior to be examined in such geographically far-removed races as *sumichrasti*, and under these circumstances even short observations provide significant details.

vation unusually low for scrub jays. To the east of the Chilpancingo area, scrub jays are unknown except for a single juvenal specimen (AM 372162) taken at La Laguna, which has been identified tentatively as a town along the Guerrero-Oaxaca border. *Remota* has also been collected at "Ftalistatipa" (AM 372160, 372161), but this locality has not been found on available maps.

TABLE 37
MEASUREMENTS OF *A. C. REMOTA*

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	19	141.8-151.5	145.58±0.58	2.58	1.77
		First-year..	6	137.8-146.5	141.67		
	F	Adult.....	9	136.9-142.0	139.89		
		First-year..	12	131.2-139.0	135.92		
Tail	M	Adult.....	19	142.5-159.0	149.48±0.91	3.98	1.99
		First-year..	6	139.7-151.4	144.83		
	F	Adult.....	9	138.7-148.6	143.56		
		First-year..	10	132.1-147.8	139.00		
Bill length	M	Adult.....	18	18.0- 21.6	19.88±0.22	0.94	4.73
	F	Adult.....	9	18.2- 19.9	18.87		
Bill depth	M	Adult.....	18	9.1- 10.2	9.69±0.06	0.27	2.79
	F	Adult.....	8	8.9- 9.5	9.15		
Bill width	M	Adult.....	19	8.2- 10.0	9.11±0.10	0.42	4.61
	F	Adult.....	9	8.1- 9.1	8.76		
Tarsus	M	Adult.....	19	40.9- 44.7	42.41±0.25	1.07	2.52
		First-year..	6	42.1- 43.9	42.60		
	F	Adult.....	9	40.8- 42.6	41.70		
		First-year..	12	39.9- 42.3	40.80		
Hind toe	M	Adult.....	19	12.9- 15.0	13.84±0.11	0.46	3.34
	F	Adult.....	9	13.1- 13.9	13.50		
Middle toe	M	Adult.....	18	19.5- 22.1	20.85±0.19	0.79	3.81
	F	Adult.....	8	19.4- 21.1	20.27		
Weights ¹ (gm.)	M	1	93		
	F	2	100-103	101.3		

¹ Reported by Davis (1944: 13).

Variation and intergradation.—Individual variation as well as sex and age differences appear to be comparable to those of other races. Under tail coverts of first-year and adult birds are consistently white. Juvenal specimens show noticeable variation in intensity of brownish-gray wash over upper breast, the lightest (MCZ 163824, BS 185533) having no more than a pale, narrow band, the darkest (MCZ 163822) having a broad, dark band over the upper chest.

Remota is most closely related to *sumichrasti* and probably intergrades with that race to the east along the Sierra Madre del Sur.

Ecologic distribution.—According to A. Starker Leopold (letter), scrub jays are common in a scrub-oak and palmetto association west of Chilpancingo between 4,500 and 6,200 feet. They do not range above the latter level, at which pine forest, inhabited by *Cyanocitta stelleri*, becomes the dominant vegetational type. According to Leopold, *remota* appears to be closely similar to Californian scrub jays in voice and behavior. Davis (1944:13) reports *remota* at 4,300 feet, 14 km. south of Chilpancingo, where he observed it to be common in wooded draws and canyons and to feed on the ground on open, grassy hillsides near by. These observations again suggest a similarity between *remota* and Californian scrub jays.

Aphelocoma coerulescens coerulescens

Description and racial characters. Male: adult fall plumage.—Upper parts: pileum, hind neck, and sides of neck dull purplish blue (Tyrian Blue); pileum fading to pale blue anteriorly and laterally on forehead and superciliary region, the latter becoming white or bluish white; auricular, subauricular, and suborbital regions also blue, but underlain with black and thus darker than neighboring neck areas; lores grayish black, with variable amount of faint gray spotting, or dusky; back dull grayish brown (Light Drab), feathers edged laterally with Smoke Gray, back thus appearing faintly streaked; scapulars and rump similar to back, but with admixture of dull blue, thus slightly darker; upper tail coverts dull blue, but lighter than head area (Light Tyrian Blue—Deep Orient Blue).

Under parts: chin, throat, and mid-chest grayish white, seemingly streaked with gray and black, an effect due to absence of barbs from terminal portions of rachises, which become black on chin, together with variable graying of lateral margins of vanes; sides of chest dull purplish blue, as above, extending toward mid-chest as pectoral collar, but becoming limited medially to lateral margins of feathers and more or less replaced by brownish gray; lower breast pale brownish gray (Smoke Gray—Pale Drab Gray), slightly darker laterally, streaked lightly and obscurely with a darker shade (Light Drab); belly similar or slightly lighter, but lacking obscure streaks and becoming white in anal area; under tail coverts dull blue (Light Tyrian Blue—Deep Orient Blue); ankle feathers Mouse Gray, with variable quantity of dull blue comparable to shade of under tail coverts.

Wings and tail: remiges, feathers of alula, and coverts dull blue (Tyrian Blue—Deep Orient Blue); primaries dull dark gray (Dark Mouse Gray) distally; inner webs of all remiges except innermost secondaries similar in color; fifth primary longest; under wing coverts dull gray (Mouse Gray), tipped with dull blue marginally; rectrices similar to remiges or slightly darker (Dark Tyrian Blue—Deep Orient Blue). Wing-tail ratio, 0.806:1. (See table 38 for other statistical data.)

Bill: black, heavy; hook small; broad basally, culmen and gonys convex.

Feet: black.

Iris: brown.

Female: adult fall plumage.—Similar to male, except for generally paler (grayer, less bluish; or lighter, less purplish) coloration and reduced markings on mid-chest; blue on middle and sides of chest reduced and replaced with dull brownish gray; pileum, hind neck, and sides of chest of slightly duller, less purplish blue (Tyrian Blue—Deep Orient Blue); under tail coverts more gray, less blue, tending to be slightly lighter (Light Tyrian Blue—Columbian Blue, or Columbian Blue); ankle feathers less bluish, more grayish.

Male and female: first-year fall plumage.—Differences between age groups parallel those in *A. c. californica*.

Male and female: juvenal plumage.—Upper parts: pileum and hind neck dull dark brown (Hair Brown—Chaetura Drab); suborbital and auricular regions slightly darker; hind neck slightly lighter, becoming lightest on back (Hair Brown—Drab, or Drab); rump, upper tail

TABLE 38

MEASUREMENTS OF *A. C. COERULESCENS* FROM EASTERN FLORIDA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	52	110.1-121.8	114.83±0.38	2.72	2.37
		First-year..	17	107.3-118.1	112.06±0.62	2.58	2.30
	F	Adult.....	41	105.3-116.3	110.20±0.42	2.70	2.44
		First-year..	27	99.3-108.9	105.00±0.50	2.61	2.48
Tail	M	Adult.....	51	132.7-151.3	142.49±0.68	4.83	3.39
		First-year..	16	128.6-142.0	135.31±1.01	4.03	2.98
	F	Adult.....	40	123.9-143.6	134.40±0.75	4.77	3.55
		First-year..	27	115.8-135.8	126.96±0.97	5.04	3.96
Bill length	M	Adult.....	50	15.8- 20.1	18.01±0.12	0.82	4.53
		First-year..	17	16.2- 19.0	17.52±0.21	0.86	4.98
	F	Adult.....	40	15.3- 18.8	17.17±0.14	0.88	5.15
		First-year..	25	14.4- 18.3	16.94±0.19	0.96	5.68
Bill depth	M	Adult.....	46	8.4- 9.9	9.22±0.05	0.35	3.82
		First-year..	16	8.9- 9.8	9.18±0.06	0.25	2.77
	F	Adult.....	37	8.0- 9.6	8.76±0.06	0.35	3.99
		First-year..	24	8.0- 9.2	8.73±0.08	0.37	4.21
Bill width	M	Adult.....	54	8.6- 10.3	9.49±0.06	0.42	4.45
		First-year..	17	8.5- 10.2	9.34±0.12	0.50	5.40
	F	Adult.....	39	8.3- 10.0	9.27±0.08	0.49	5.33
		First-year..	25	8.2- 9.8	9.05±0.08	0.42	4.64
Tarsus	M	Adult.....	54	34.7- 40.3	37.23±0.18	1.32	3.54
		First-year..	17	35.0- 39.7	36.93±0.26	1.09	2.95
	F	Adult.....	41	33.6- 38.8	36.33±0.20	1.25	3.44
		First-year..	26	33.4- 37.9	35.70±0.21	1.06	2.98
Hind toe	M	Adult.....	54	11.1- 13.4	12.37±0.07	0.50	4.04
		First-year..	17	11.5- 13.3	12.48±0.10	0.42	3.37
	F	Adult.....	41	11.4- 13.0	12.26±0.06	0.39	3.16
		First-year..	27	11.1- 12.7	12.04±0.09	0.40	4.09
Middle toe	M	Adult.....	54	17.4- 20.7	18.80±0.08	0.62	3.29
		First-year..	17	16.7- 19.4	18.52±0.15	0.61	3.29
	F	Adult.....	41	17.1- 20.0	18.22±0.10	0.65	3.59
		First-year..	27	16.6- 19.7	18.00±0.14	0.77	3.90

coverts, scapulars, and lesser and middle wing coverts Hair Brown; pileum may be tinged lightly with dull grayish blue; superciliary line obsolescent (dull brown, lighter than neighboring areas) or lacking.

Under parts: chin and throat dull white (approaching Pale Smoke Gray); sides of throat and upper chest dull brown (Hair Brown—Drab), extending across upper chest to form broad, indistinct band, narrowest in mid-region; lower breast and sides of belly light dull brownish gray (Smoke Gray—Drab Gray), becoming whitish in anal region; under tail coverts and ankle feathers dull brownish gray (Mouse Gray).

Wings and tail: remiges duller than in adults (Delft Blue—Tyrian Blue); distal portions of

TABLE 39
MEASUREMENTS OF *A. C. COERULESCENS* FROM WESTERN FLORIDA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	16	112.2-120.1	115.44±0.60	2.40	2.08
		First-year..	8	106.6-116.1	110.62		
	F	Adult.....	19	105.7-114.5	110.42±0.62	2.72	2.46
		First-year..	11	101.6-111.3	106.27		
Tail	M	Adult.....	16	135.6-154.4	142.31±1.35	5.41	3.79
		First-year..	7	125.9-141.8	133.86		
	F	Adult.....	19	124.3-140.4	134.32±1.05	4.58	3.42
		First-year..	11	123.4-138.6	129.09		
Bill length	M	Adult.....	16	16.7- 20.4	17.93±0.24	0.98	5.47
		First-year..	8	17.2- 18.8	17.61		
	F	Adult.....	19	16.7- 18.9	17.47±0.15	0.67	3.83
		First-year..	11	15.6- 18.4	16.71		
Bill depth	M	Adult.....	14	8.3- 10.0	9.15±0.11	0.41	4.44
		First-year..	8	9.0- 9.6	9.33		
	F	Adult.....	18	8.3- 9.5	8.85±0.08	0.36	4.05
		First-year..	10	8.4- 9.2	8.77		
Bill width	M	Adult.....	15	8.7- 10.2	9.32±0.10	0.38	4.12
		First-year..	8	8.7- 9.8	9.15		
	F	Adult.....	19	8.2- 10.0	8.97±0.11	0.50	5.54
		First-year..	11	8.5- 9.4	8.87		
Tarsus	M	Adult.....	16	35.7- 38.9	37.08±0.22	0.86	2.32
		First-year..	8	36.0- 39.5	37.26		
	F	Adult.....	19	34.0- 38.0	36.10±0.26	1.13	3.14
		First-year..	11	34.5- 37.7	36.29		
Hind toe	M	Adult.....	16	11.3- 13.1	12.48±0.12	0.47	3.75
		First-year..	8	11.5- 13.3	12.35		
	F	Adult.....	18	11.2- 12.6	12.10±0.07	0.32	2.60
		First-year..	11	11.4- 12.7	11.95		
Middle toe	M	Adult.....	16	17.8- 19.7	18.69±0.14	0.56	3.02
		First-year..	8	17.7- 19.5	18.81		
	F	Adult.....	19	16.8- 19.0	17.99±0.15	0.66	3.68
		First-year..	11	17.1- 18.9	17.88		
Weights ¹ (gm.)	M	2	76 - 80	78.3		
	F	1	70		

¹ Reported by Amadon (1944b:1).

primaries and inner webs of all except innermost secondaries dull dark brown, as in adults, or slightly lighter; middle and marginal wing coverts dull brown (Hair Brown), but those nearest margin blue; greater wing coverts and feathers of alula similar to remiges, but tinged distally with dull brown; rectrices similar to remiges in color.

Bill and feet: varying shades of brown and brownish black, depending on age.

Individual variation.—In adult males the chief variable in the color of the under parts is the quantity of blue in the collar. At one extreme are variants (AM 372063) with a conspicuous semicircular band of blue; at the other are variants (MCZ 303864) almost lacking blue in the mid-region of the collar. Variation in color of throat, lower breast, belly, and under tail coverts is negligible. Rarely, the under tail coverts are lighter than described above, becoming Light Columbian Blue (MCZ 201197). Dorsally, some variation is seen in the extent of lightened coloration over the forepart of the head. Typically the blue becomes lighter from the mid-crown region anteriorly and laterally; but the whole crown area may be lighter than the nape or the sides of the neck (MVZ 82434). Among fresh-plumaged specimens there is only slight variation in color of the back; occasional variants are lighter (with more Smoke Gray) than described above; there may also be an overcast of blue, especially along the collar margin between nape and back, which is then indistinct (MCZ 201196).

When compared with adult males in series, first-year males are seen to differ in that their average shade of blue is duller (grayer) and less purplish. The collar pattern of most individuals compares with that of most adult males, but none is so richly colored as that of extremes among adults, and more approach the other extreme. The same observation is to be made of the color of head plumage and under tail coverts.

The collar of adult females, although less blue than that of adult males, retains at least some blue in the weakest-colored variants (MCZ 15178); in first-year females, blue collar markings are usually absent (MCZ 203608). The slightly lighter and duller under tail coverts of adult females are Tyrian Blue—Columbian Blue, or Columbian Blue; those of first-year females are Columbian Blue, or Columbian Blue—Light Columbian Blue (C 23723). Similarly, ankle feathers are less blue and more gray; in first-year females they are Mouse Gray, usually without any tinge of blue. Color of pileum in first-year females may be similar to that of adult females (Tyrian Blue—Deep Orient Blue, as in MCZ 203608) or slightly less purplish (Deep Orient Blue, as in C 23723). No significant variation is evident in color of back or, excepting collar and under tail coverts, under parts.

Geographic distribution.—Peninsular Florida, from coastal Duval (St. Johns River), Alachua (Micanopy), Gilchrist (Wannee), and Dixie (Pine Point) counties, south along the east coast to Dade County (Rockdale) and along the west coast to Collier County (Naples, Immokalee); south of Orange County, absent inland along the eastern coast and extending eastward from the western coast to Highlands (Lake Istokpoga) and Glades (Fisheating Creek) counties. The definition of range provided above does not differ in any important respect from that of Howell (1932:339). All localities cited here and not represented in the list of specimens (p. 407) are taken from Howell.

The present-day distribution of scrub jays in Florida is irregular (Howell, *ibid.*), owing in part, of course, to the natural interruptions of the characteristic habitat, but as well to the continued clearing of scrubland (Grimes, 1940:435) so that the total areal range is being reduced noticeably.

The only extralimital record which has come to my notice is that of an adult female (MCZ 15178) taken at Key West on December 27, 1893. The facts that this

is an adult bird and that the scrub jay is typically a comparatively sedentary species (Grimes, *ibid.*) lead me to doubt that this specimen represents a true vagrant. The distance between Key West and the nearest known point of marginal

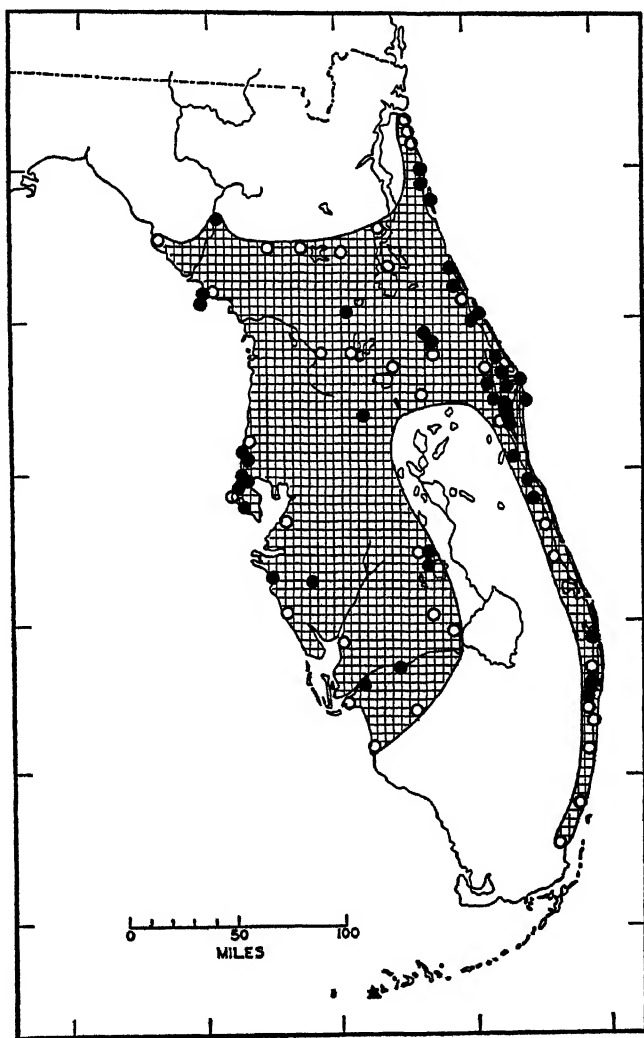


Fig. 12. Distribution of *Aphelocoma c. coerulescens* in Florida. Dots indicate localities represented by specimens; circles, localities reported in the literature; triangles, vagrants.

occurrence is about 120 miles, measured along the Florida Keys lying between the two points. The specimen in question may have been a caged bird that escaped.

Geographic variation.—On the basis of the peculiar distributional pattern of the Floridan scrub jay (see fig. 12), the available specimens were divided into two groups representing eastern and western populations connected across the northern third of the peninsula. Such a division seemed desirable, further, because about

75 per cent of the specimens have been collected along the eastern coast and 55 per cent in Volusia and Brevard counties alone. Thus the specimens from these two counties provide good evidence of population variability in this isolated race of *Aphelocoma coerulescens*. The data representing the other 20 per cent have been combined with those from Volusia and Brevard counties. These two sets of data were compatible with each other and statistical computations based on the restricted sample from Volusia and Brevard counties were not affected in any significant way by the combination.

Examination of tables 38 and 39 reveals that there are no significant differences between eastern and western populations. No evidence of geographic variation in color was detected.

Ecologic distribution.—The Floridan scrub jay has long been identified with a type of scrub vegetation (Mulvania, 1931:529) characteristic of peninsular Florida. It was noted early that the local distribution of the species follows that of scrub, and that it is not found in pine woods, hummocks, or swamps (Allen, 1871:299). The characteristic habitat is a low, dense, semixeric thicket usually not exceeding 10 feet in height and commonly dominated by oaks (*Quercus geminata*, *Q. myrtifolia*), sword palmetto (*Serenoa serrulata*), dwarf wax myrtle (*Myrica pumila*), and scattered, stunted pines (*Pinus clausa* or *P. caribaea*) (Bendire, 1895:370; Amadon, 1944b:2). However, it is the edges of such scrub bordering on small openings or clearings that answer the habitat requirements of the scrub jay (Bryant, 1859:9) rather than the uninterrupted mass of dense vegetation. Most of the feeding of this species occurs on open ground bordering scrub (Amadon, *ibid.*).

Nests are placed at heights of 2 to 12 feet (Howell, 1932:339), most commonly in oaks (Bryant, 1859:9; Bailey, 1925:93; Grimes, 1932:61) and myrtle (Grimes, 1932:61, 1940:432; Amadon, 1944b:8). Occasionally they are placed in rose thickets (Smith, 1940:7), grapefruit trees (Bailey, 1925:93), wax myrtle and wild olive (Grimes, 1932:61, 1940:431), dwarf holly (*Ilex myrtifolia*), and jasmine vines (*Jasminum grandiflorum*) (Amadon, 1944b:8), and sand pine (*P. clausa*) (Howell, 1932:339).

VARIATION AND INTERRELATIONSHIPS AMONG RACES OF *APHELOCOMA ULTRAMARINA*

The Mexican jay, *Aphelocoma ultramarina*, consists of seven races which are here tentatively divided into three groups on the basis of both color and mensural characters and evidence of geographic separation. The distribution of *A. ultramarina* through the Sierra Madre Occidental, Sierra Madre Oriental, and connecting ranges in the southern part of the Mexican plateau forms a roughly U-shaped range which reaches into the United States in southwestern Texas and in southeastern Arizona and southwestern New Mexico.

The first, or "*wollweberi*," group of races occupies the western arm of this range. The races are, from north to south, *arizonae*, *wollweberi*, and *gracilis*. All are relatively pale in dorsal coloration. *Gracilis* represents the small extreme of a north-south size cline; it is also the smallest race in the species as a whole and in this respect contrasts markedly with the geographically adjacent member of another group, the race *colimae*.

The second, or "*sordida*," group of races occupies the eastern arm of the geographic range. The races, north to south, are *couchii* and *sordida*. Both are dark-colored. *Sordida* is the large extreme of a north-south size cline, but considered in the species as a whole the races are relatively small to intermediate in size. The group is further characterized by blackening of the bill before completion of the postjuvénal molt.

The third, or "*ultramarina*," group occupies the base of the U-shaped range. The races, east to west, are *ultramarina* and *colimae*. These races are also more or less dark-colored, but are separable from the "*sordida*" group by a striking size differential. (For details see p. 340.) Further, in the "*ultramarina*" group the lower mandible may remain light-colored for several years (Pitelka, 1945b: 257).

A difference which separates at least *couchii* from *arizonae* is the fact that the eggs of the former are spotted, those of the latter unspotted (Van Tyne and Sutton, 1937: 61). The bearing of this difference on the separation of groups of races cannot be determined, since no data on egg color are available for the Mexican races.

No conclusive evidence is yet available for the presence or absence of geographic contact among the three groups. Presumably, if such contact occurs, it does so in Zacatecas and possibly Guanajuato and northeastern Jalisco. Evidence of intergradation between them in specimens available to me is only suggestive. Geographic contact almost certainly occurs in Hidalgo between the "*sordida*" and "*ultramarina*" groups, but the evidence from morphological characters indicates that there is at least partial separation of the groups. Nothing is known of the nature of this separation.

Discussions of racial characters in the following accounts rest on the representatives of the species, the races *arizonae* and *couchii*, for which the most extensive series of specimens are available.

THE "WOLLWEBER" GROUP OF RACES

Aphelocoma ultramarina arizonae

Description and racial characters. Male: adult fall plumage.—Upper parts: pileum, hind neck, and sides of neck dull blue (Deep Orient Blue); suborbital and subauricular regions also dull blue but darker; auricular region brownish black, overcast variably with blue; lores black; nasal feathers dull blue; back brownish gray (Mouse Gray) overcast with variable amount of dull blue; scapulars and rump more blue than back; upper tail coverts light dull blue (Alice Blue).

Under parts: chest light dull brownish gray (Light Drab or Light Drab—Smoke Gray); throat lighter (Pale Mouse Gray or Pale Neutral Gray) than chest; shafts of chin feathers dark, as in *A. coerulescens*, but less conspicuously so; chest variably overcast with light dull blue forming an obscure broad band extending from sides of neck across upper chest; shafts of breast feathers slightly darker than vanes, breast thus faintly streaked; ankle feathers light brownish gray (Mouse Gray—Light Mouse Gray); belly and under tail coverts white.

Wings and tail: remiges, greater coverts, and feathers of alula dull blue (Cadet Gray—Parula Blue); primaries dull dark brown (Fuscous) distally; inner webs of all remiges except innermost secondaries similar in color; fourth, fifth, or sixth secondaries longest, all closely similar in length; middle and marginal coverts slightly brighter than greater coverts (still closest to Cadet Gray—Parula Blue); under wing coverts dull gray (Light Mouse Gray to Mouse Gray), darker and tinged with light blue marginally; rectrices similar to remiges in color. Wing-tail ratio, 1.127:1. (See table 40 for other statistical data.)

Bill: black, moderately heavy, and pointed; curvature of culmen and gonys approximately equal; varying, usually small, amounts of light color on lower mandible in second- and third-year birds (Pitelka, 1945b:256).

Feet: black.

Iris: brown.

Female: adult fall plumage.—Similar to male, but averaging slightly duller in blue coloration of head and less blue on chest. Usually smaller in all measurements (see tables 40 and 41), most differences falling between 1 and 5 per cent.

TABLE 40

MEASUREMENTS OF ADULTS OF *A. U. ARIZONAE* FROM CHIRICAHUA MOUNTAINS, ARIZONA

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	19	160-174	166.1 \pm 0.7	3.2	1.9
	F	16	156-169	160.1 \pm 1.0	4.0	2.5
Tail	M	19	143-157	147.3 \pm 0.7	3.2	2.2
	F	16	135-151	141.9 \pm 1.2	4.7	3.3
Bill length	M	19	18.2-22.8	20.83 \pm 0.25	1.08	5.18
	F	15	18.1-22.2	20.24 \pm 0.32	1.25	6.20
Bill depth	M	19	9.5-11.0	10.22 \pm 0.10	0.43	4.16
	F	14	9.6-10.5	9.94 \pm 0.07	0.27	2.72
Bill width	M	19	8.3- 9.8	8.93 \pm 0.11	0.49	5.47
	F	16	8.1- 9.1	8.68 \pm 0.07	0.29	3.37
Tarsus	M	19	39.7-44.0	42.25 \pm 0.21	0.91	2.15
	F	16	39.5-43.3	41.36 \pm 0.25	0.98	2.38
Hind toe	M	19	14.3-15.7	14.98 \pm 0.10	0.42	2.82
	F	16	13.8-15.6	14.75 \pm 0.12	0.46	3.13
Middle toe	M	19	20.2-21.6	20.85 \pm 0.10	0.46	2.20
	F	16	19.2-21.7	20.52 \pm 0.13	0.74	3.61

Male and female: first-year fall plumage.—Similar to adult except that remiges and rectrices of juvenal plumage are retained through postjuvenal molt, as are also greater primary coverts, greater and middle secondary coverts in variable number, and feathers of alula; blue areas average slightly duller than those of adults of corresponding sex; chest overcast with less blue; first-year males approximately comparable to adult females in color. First-year males smaller than adults of corresponding sex; wing and tail shorter in first-year males than in adults of either sex.

Male and female: juvenal plumage.—Upper parts: pileum, auricular and suborbital regions, hind neck, sides of neck, and upper tail coverts dull brownish gray (Mouse Gray); pileum overcast variably and usually only slightly with dull blue; back, scapulars, and wing coverts (but not greater coverts) similar (Mouse Gray) or somewhat browner (Mouse Gray—Light Drab); lores brownish black.

Under parts: chest light dull brownish gray (Light Drab); throat slightly lighter (Light Mouse Gray); remaining under parts dull white.

Wings and tail: remiges duller than in adults (Cadet Gray to Deep Green-Blue Gray); distal portions of primaries and inner webs of all except innermost remiges dull dark brown, slightly lighter than in adults; middle and marginal coverts dull brownish gray (Mouse Gray);

greater coverts and feathers of alula similar to other coverts, but more bluish and approaching, but duller than, color of remiges.

Bill: lower mandible except tip and basal half of upper mandible light-colored (yellow or yellowish in dried specimens, flesh-colored in life; see Pitelka, 1945b:256); dark terminally.

Feet: varying shades of brown depending on age, becoming black before completion of post-juvenal molt.

Individual, sex, and age variation.—Among fresh-plumaged males of *A. u. arizonae*, variation in blue coloration of the head is not so great as in *A. coerulescens*. Only occasional specimens deviate from Deep Orient Blue, some approaching Tyrian Blue (BS338893), others Parula Blue (MVZ81355). Color of back varies in the amount of blue overcasting the gray, from slight (DC 12340) to heavy (MVZ

TABLE 41
AVERAGE MEASUREMENTS OF SEX AND AGE GROUPS OF *A. ULTRAMARINA* EXPRESSED
AS PERCENTAGE OF MEASUREMENTS OF ADULT MALES

	Males, first-year	Females			
		Adult			First-year
From table no.	44	40	43	44	44
Wing..	95.7	96.4	98.0	98.2	95.0
Tail.....	96.2	96.3	97.3	97.5	95.4
Bill length.....	96.7	97.2	97.1	97.8	94.9
Bill depth.....	96.4	97.3	97.8	96.3	93.2
Bill width.....	98.6	97.2	94.8	94.2	97.9
Tarsus.....	99.9	97.9	98.9	100.1	99.0
Hind toe.....	99.5	98.5	99.3	100.1	97.1
Middle toe.....	98.7	98.4	99.8	98.8	96.1

81355); some overcast is always evident. Under parts vary in extent of white over lower breast and belly; white may extend onto the lower breast (DC 27772) or it may be restricted to the anal region (CAS 30657). Typically there is a more or less gradual transition in color from the brownish-gray wash of the breast to the white belly; when, however, the lower breast is white, a more or less sharp boundary exists between the dark, broad band of the upper chest and the lighter, lower chest (e.g., BS 205612). Shafts of breast feathers are usually darker than the vanes (CAS 30657), but occasionally the breast is uniformly colored (DC ex-28). Typically the throat coloration is slightly lighter than that of the chest, and it lacks a blue overcast as well (MVZ 81355). An irregular, asymmetric area of white, variable in size, occurs on the gray throat of five of twenty-three fresh-plumaged adult males (CM 30236 and 142579, USNM 127838; see table 47). In adult males and all remaining age and sex classes, these white areas vary from a few white feathers to a spot covering more than half of the throat, but never, in *arizonae*, the entire throat. There is, moreover, variability in the intensity of throat coloration in specimens lacking white. In the majority of them (table 47) the throat is slightly lighter than the chest area and without an overcast of dull blue; but in a few specimens the throat is as dark as the chest and, in a slightly greater proportion, the throat

is whitish and contrasts with the chest in color. Within sex and age classes other than adult males, individual variation in color is of a similar order.

Variation due to sex and age is not so pronounced in *A. ultramarina* as in *A. coerulescens*. First-year males do not appear to differ from adult females in color. Blue areas of most individuals of both groups fall near Parula Blue—Deep Orient

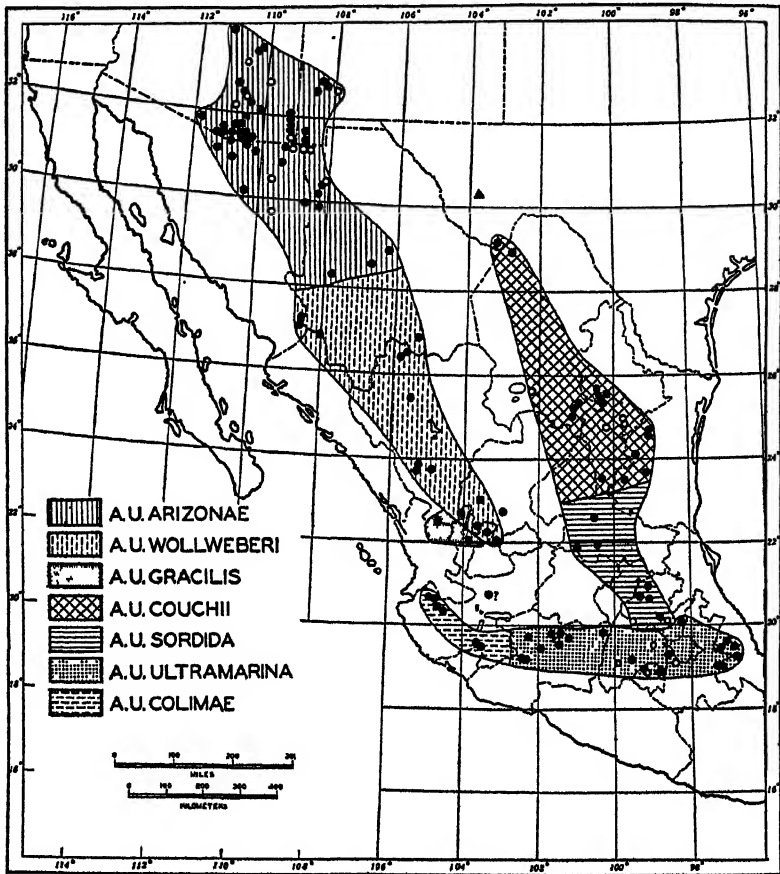


Fig. 13. Distribution of races of *Aphelocoma ultramarina*. Dots indicate localities from which specimens have been examined; circles, localities reported in the literature; squares, type localities; triangles, vagrants.

Blue (CAS 38909). Duller extremes approach Parula Blue—Cadet Gray (CS 8039, a first-year male; USNM 128037, JEL 2920, both adult females). Among adult females, occasional dark variants approach Parula Blue—Light Tyrian Blue (CAS 30000). First-year females, averaging slightly duller than adults, approach Cadet Gray—Parula Blue (MVZ 33801; CM 142569). Color of back and under parts does not differ significantly among age and sex groups except that the blue overcast of the chest averages less in first-year males and adult females, and in first-year females it is still smaller in amount or is lacking.

Among juveniles, color variation is comparable in degree to that observed in *A.*

coerulescens. Two juveniles (MVZ 58956, 58957), indicated in table 47 as having dark throat coloration, were both collected two miles west of Santa Rita, Grant County, New Mexico, in August, 1931, from different family groups. One of these (58957) is noteworthy in that its head is overcast dorsally with an unusual amount

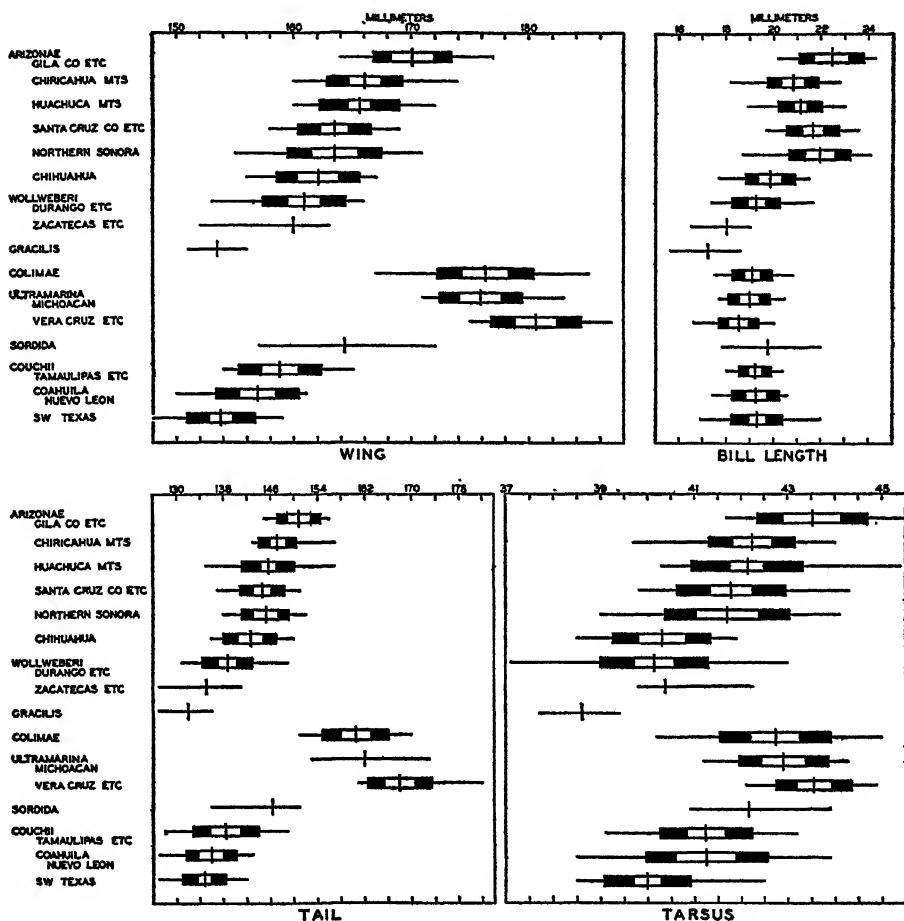


Fig. 14. Individual and geographic variation in races of *Aphelocoma ultramarina*. Data arranged in north-to-south, thence west-to-east, and south-to-north order; data based on adult males.

of blue; further, the throat as well as the chest is overcast with a slight amount of blue.

Light coloration of the bill in *arizonae* is gradually reduced to occupy proximal parts of the lower mandible and it disappears during a period of from less than one year to more than two years. In males the bill tends to become black slightly more rapidly than in females. For details see Pitelka, 1945b:257.

Geographic distribution.—Southeastern Arizona and southwestern New Mexico, from the Baboquivari Mountains, Pima County, Sierra Ancha, Gila County, and Santa Rita, Grant County, south and east into northern Sonora (Sierra de San

Antonio, Sierra de Oposura, van Rossem, 1945:173) and northwestern Chihuahua (thirty miles west of Miñaca, seven miles west of Sauz).

The only extralimital record known to me is that of a specimen taken in March, 1906, near Mount Jesus, in Clark County, Kansas (Keith, 1940:427). The beak

TABLE 42

MEASUREMENTS OF ADULTS OF *A. U. ARIZONAE* FROM SOUTHEASTERN ARIZONA
(Gila, Pinal, Southern Navajo, Northeastern Pima, and Northwestern Cochise Counties)

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	14	164-177	170.1±0.9	3.3	1.9
	F	12	158-169	162.5±1.0	3.4	2.1
Tail	M	13	145-156	150.9±1.0	3.6	2.4
	F	12	134-147	142.0±1.0	3.6	2.5
Bill length	M	13	20.2-24.3	22.44±0.37	1.35	6.02
	F	12	19.5-22.0	20.75±0.18	0.62	2.99
Bill depth	M	12	10.3-10.9	10.43±0.07	0.25	2.42
	F	11	9.4-10.3	9.90±0.08	0.27	2.73
Bill width	M	14	8.8-9.8	9.26±0.09	0.33	3.52
	F	12	8.2-9.5	9.07±0.11	0.40	4.37
Tarsus	M	14	41.7-46.3	43.53±0.31	1.16	2.67
	F	12	41.2-44.5	42.62±0.31	1.06	2.49
Hind toe	M	14	14.8-16.6	15.44±0.13	0.47	3.05
	F	12	14.6-16.1	15.22±0.13	0.45	2.96
Middle toe	M	14	20.2-23.3	21.18±0.15	0.52	2.48
	F	12	20.1-22.1	21.66±0.23	0.85	3.92
Weights ¹ (gm.)	M	8	127-151	135.6		
	F	5	131-164	142.5		

¹ Adults only, collected in late April; three of the females collected in egg-laying period.

of this specimen is stated to have a "whitish band encircling the base." This fact together with the date of collection indicates that the individual was almost certainly a first-year bird.

Southward through east-central Sonora and west-central Chihuahua, distribution of *A. ultramarina* is more or less continuous along the Sierra Madre Occidental (fig. 13). Intergradation between *arizonae* and *wollweberi* to the south is gradual (see p. 331), but no specimens are available to me from localities between latitudes 27° N and 28° 15' N; the line separating the two races is thus arbitrary, pending critical study of specimens from this area.

Geographic variation and intergradation.—There is no evidence of geographic variation in color over the range of *arizonae* in Arizona, New Mexico, and Sonora. A series of specimens from the San José and Baboquivari mountains suggests that

TABLE 43

MEASUREMENTS OF A. U. ARIZONAE FROM HUACHUCA MOUNTAINS, COCHISE COUNTY, ARIZONA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	41	160-172	165.6 \pm 0.5	3.4	2.0
		First-year..	10	152-165	156.7		
	F	Adult.....	28	155-168	162.3 \pm 0.8	4.0	2.4
		First-year..	7	147-157	152.7		
Tail	M	Adult.....	42	135-157	145.7 \pm 0.7	4.5	3.1
		First-year..	11	130-145	139.0		
	F	Adult.....	28	132-150	141.8 \pm 1.0	5.1	3.6
		First-year..	7	128-141	135.4		
Bill length	M	Adult.....	42	19.0-23.0	21.13 \pm 0.14	0.92	4.35
		First-year..	7	18.8-22.5	20.63		
	F	Adult.....	29	18.3-22.6	20.51 \pm 0.20	1.09	5.34
		First-year..	6	18.3-22.2	19.85		
Bill depth	M	Adult.....	41	9.3-11.2	10.24 \pm 0.07	0.47	4.61
		First-year..	7	9.8-10.4	10.05		
	F	Adult.....	27	9.2-10.8	10.01 \pm 0.08	0.42	4.19
		First-year..	5	9.8-11.0	10.37		
Bill width	M	Adult.....	41	8.4-10.5	9.31 \pm 0.08	0.50	5.32
		First-year..	7	8.4-9.6	9.02		
	F	Adult.....	28	8.0-9.5	8.83 \pm 0.07	0.39	4.47
		First-year..	6	8.2-9.3	8.65		
Tarsus	M	Adult.....	43	40.3-45.4	42.14 \pm 0.18	1.19	2.83
		First-year..	11	39.5-43.0	41.55		
	F	Adult.....	29	38.8-44.4	41.71 \pm 0.26	1.43	3.42
		First-year..	7	37.1-42.6	40.40		
Hind toe	M	Adult.....	43	14.0-16.1	14.95 \pm 0.07	0.48	3.19
		First-year..	11	14.1-15.5	14.87		
	F	Adult.....	29	13.6-15.7	14.85 \pm 0.09	0.47	3.15
		First-year..	7	12.7-15.6	14.28		
Middle toe	M	Adult.....	42	19.5-21.9	20.80 \pm 0.09	0.60	2.87
		First-year..	11	20.3-22.1	20.94		
	F	Adult.....	29	19.6-22.3	20.75 \pm 0.10	0.56	2.70
		First-year..	7	19.6-21.2	20.20		

slightly lighter variants occur in greater numbers along the west margin than in other parts of the range of *arizonae*, but this is only a barely perceptible trend.

Southeastward, in Chihuahua, darker variants indicate intergradation with *wollweberi*. Specimens from central Chihuahua (for example, a series taken at thirty miles west of Miñaca) are more or less intermediate between *arizonae* and *wollweberi* in dorsal coloration, but the under parts are dark as in *arizonae*. Five juveniles from Chihuahua are slightly darker (brownier) dorsally than *arizonae*;

TABLE 44
MEASUREMENTS OF *A. U. ARIZONAE* FROM SOUTHEASTERN PIMA AND SANTA CRUZ
COUNTIES, ARIZONA

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	24	153-169	163.5 \pm 0.6	3.1	1.9
		First-year..	9	150-162	156.4		
	F	Adult.....	16	156-167	160.5 \pm 0.9	3.4	2.1
		First-year..	14	149-161	155.2		
Tail	M	Adult.....	24	137-151	144.6 \pm 0.8	3.7	2.6
		First-year..	9	134-149	139.1		
	F	Adult.....	14	134-149	140.9 \pm 1.1	4.0	2.8
		First-year..	13	128-147	138.0		
Bill length	M	Adult.....	23	19.7-23.6	21.67 \pm 0.23	1.11	5.10
		First-year..	8	19.0-22.1	20.95		
	F	Adult.....	16	18.1-23.8	21.19 \pm 0.27	1.09	5.12
		First-year..	9	17.8-23.5	20.57		
Bill depth	M	Adult.....	25	9.6-11.2	10.31 \pm 0.08	0.38	3.71
		First-year..	7	9.3-10.5	9.94		
	F	Adult.....	17	9.5-10.7	9.93 \pm 0.08	0.35	3.52
		First-year..	9	9.4-10.1	9.61		
Bill width	M	Adult.....	24	8.4-9.9	9.13 \pm 0.09	0.45	4.97
		First-year..	8	8.5-9.7	9.00		
	F	Adult.....	17	7.5-9.6	8.60 \pm 0.11	0.47	5.49
		First-year..	9	8.0-9.5	8.94		
Tarsus	M	Adult.....	25	39.8-44.3	41.80 \pm 0.23	1.16	2.78
		First-year..	9	39.5-45.1	41.77		
	F	Adult.....	17	40.0-43.6	41.85 \pm 0.19	0.76	1.83
		First-year..	13	39.0-43.5	41.44		
Hind toe	M	Adult.....	25	14.0-16.3	14.98 \pm 0.11	0.57	3.82
		First-year..	9	14.3-15.7	14.90		
	F	Adult.....	17	13.8-16.2	14.99 \pm 0.15	0.61	4.06
		First-year..	14	14.0-15.2	14.54		
Middle toe	M	Adult.....	25	19.8-23.0	21.15 \pm 0.15	0.74	3.49
		First-year..	9	20.0-22.3	20.87		
	F	Adult.....	17	19.8-22.1	20.90 \pm 0.16	0.68	3.23
		First-year..	14	18.6-21.6	20.33		

the back of the darkest of these (BS 165524, Colonia García) is Drab—Hair Brown. The area of intergradation extends southward into southeastern Sonora and north-eastern Sinaloa, from where, however, specimens are closer to *wollweberi*.

Variation in size represents, in *arizonae*, the northern terminus of a cline which extends southward to include the populations of *wollweberi* and *gracilis*. Specimens obtained along the northeastern and northern margins of the range of *arizonae* (tables 40 and 42, respectively) represent a large extreme. Southward, all dimen-

sions become progressively smaller (fig. 14). Specimens from the Baboquivari Mountains, the westernmost part of the range of *arizonae*, are visibly smaller than those from the Chiricahua Mountains and the Sierra Ancha to the east and north, respectively, but they do not differ significantly from those of a large series from Santa Cruz and southeastern Pima counties and are best regarded as marginal

TABLE 45
MEASUREMENTS OF ADULTS OF *A. u. arizonae* FROM NORTHERN SONORA

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	16	155-171	163.5 \pm 1.0	4.0	2.5
	F	12	148-166	159.8 \pm 1.6	5.6	3.5
Tail	M	15	138-152	145.3 \pm 1.1	4.1	2.8
	F	12	128-149	138.6 \pm 1.7	6.0	4.3
Bill length	M	16	18.7- 24.1	21.96 \pm 0.32	1.29	5.87
	F	12	18.2- 23.8	20.78 \pm 0.43	1.50	7.51
Bill depth	M	15	9.8- 10.5	10.21 \pm 0.05	0.20	1.98
	F	12	9.3- 10.7	9.88 \pm 0.12	0.42	4.25
Bill width	M	15	8.1- 10.4	9.10 \pm 0.16	0.64	7.03
	F	9	8.4- 9.6	9.05 \pm 0.10	0.33	3.65
Tarsus	M	16	39.0- 44.1	41.71 \pm 0.34	1.34	3.21
	F	12	39.2- 43.0	41.32 \pm 0.33	1.14	2.77
Hind toe	M	16	14.0- 15.7	14.79 \pm 0.12	0.47	3.20
	F	12	13.9- 15.7	14.80 \pm 0.15	0.53	3.55
Middle toe	M	15	19.9- 22.2	20.82 \pm 0.17	0.65	3.14
	F	12	19.9- 22.2	20.82 \pm 0.19	0.64	3.08
Weights ¹ (gm.)	M	9	104-133	120.8		
	F	9	109-132	115.7		

¹ Including data from specimens taken in southern Santa Cruz County, Arizona, and northwestern Chihuahua.

representatives of populations immediately to the east, which, in turn, represent a segment in the size cline described above.

Each of five, or 28 per cent, of eighteen unworn or moderately worn specimens from Chihuahua has an area of white on the throat; this percentage is slightly higher than that for typical *arizonae* (table 47), and although the data are too limited to be more than suggestive, they indicate a trend toward *wollweberi*, in which the throat is white or almost entirely so.

Ecologic distribution.—*A. u. arizonae* is characteristically associated with live-oak woodland at elevations ranging from 3,000 to 7,500 feet, but mainly from 4,000 to 6,000 feet (Scott, 1886:81; Swarth, 1904:31). More than 30 nests are reported from oaks at heights of 10 to 30 feet and usually of about 15 feet (Bendire, 1887:554; Scott, *op. cit.*). Vagrants have been observed in bottom-land growths below

the normal altitudinal range along the Sonoita (Swarth, 1929:312) and Santa Cruz (Vorhies *et al.*, 1935:246) rivers. Oberholser's (1930:93) record of a specimen collected in October at 9,000 feet suggests that there may be a slight dispersal to higher elevations after the breeding season.

Virtually no information is available in the literature on the interspecific relations of *A. ultramarina* with *A. coerulescens* and *Cyanocitta stelleri*. The statement of Swarth (1904:31) that individuals of all three species were observed to feed together indicates that under certain circumstances, at least, habitat distribution of all three may overlap. Some overlap with a fourth species of jay, *Gymnorhinus*

TABLE 46
MEASUREMENTS OF ADULTS OF *A. U. ARIZONAE* FROM NORTHWESTERN CHIHUAHUA

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	16	156-167	162.1 \pm 0.9	3.5	2.1
Tail	M	16	136-150	142.6 \pm 1.1	4.5	3.2
Bill length	M	16	17.7-21.5	19.86 \pm 0.26	1.05	5.28
Bill depth	M	15	9.1-10.9	9.97 \pm 0.14	0.55	5.52
Bill width	M	16	8.3-9.6	9.04 \pm 0.09	0.36	4.03
Tarsus	M	16	38.5-41.9	40.31 \pm 0.26	1.05	2.61
Hind toe	M	16	13.6-15.2	14.36 \pm 0.10	0.40	2.78
Middle toe	M	16	19.0-20.6	19.88 \pm 0.14	0.55	2.75

cianocephalus, also occurs in certain sections of east-central Arizona where the latter species reaches the southern limits of its breeding distribution.

Habitat distribution of jays in east-central Arizona was studied at two localities in that region during the period from April 22 to 29, 1949. At Sawmill, 5,600 feet, Gila County, *arizonae* was common and *Cyanocitta stelleri* and *Gymnorhinus cyanocephalus* also occurred as resident species. The habitat most frequented by *arizonae* was woodland of only moderately open type composed of oaks, junipers, pine (*Pinus ponderosa*), and various shrubs (including *Arctostaphylos* and *Ceanothus*), with a ground cover of herbs and grasses in which the jays foraged. Groups of twelve to twenty individuals were spaced out through suitable habitat and possibly occupied mutually exclusive areas. Several such groups were observed repeatedly to be present in their respective areas and to follow certain general routes in traversing those areas. In the course of these local wanderings, *arizonae* entered the open forests of yellow pine occupied by *Cyanocitta* or, on the other hand, the parkland stands of pine and oak occupied by *Gymnorhinus*; but *arizonae* occurred in the latter habitats only briefly, and then only along its margins, never in the most open areas ordinarily traversed by *Gymnorhinus*. Thus the headquarters of *arizonae* were the mixed oak-pine-juniper woodlands and specifically such wood-

lands in which the scattered pines rose above the other vegetation. *Gymnorhinus* entered the margins of such vegetation en route to other areas, stopping to forage occasionally if flat, more or less grassy areas occurred in the given woodland stand. *Cyanocitta* entered woodland of average density where pines were present or which adjoined pine stands used as headquarters by that species. Thus, *arizonae* overlapped with both *Cyanocitta* and *Gymnorhinus* in habitat distribution, but the two latter forms, at least in the Sawmill area in mid-spring, did not do so.

That tall though scattered pines are an essential component of the habitat of at least the northwestern populations of *A. ultramarina* was indicated by observations south of Whiteriver, 6,100 feet, Navajo County. Here *arizonae* occurred only locally, evidently at the upper altitudinal margins of its breeding range. Only two

TABLE 47
THROAT COLOR IN *A. U. ARIZONAE* FROM SONORA, ARIZONA, AND NEW MEXICO

	Dark	Light	Whitish	White area
Collected in September, October, and November				
Adult males.....	0	19	4	5
First-year males.....	0	11	1	0
Adult females.....	1	8	1	6
First-year females.....	2	11	1	5
Juveniles.....	2	9	1	4
Totals.....	71			20
Percentage.....	78			22

groups of jays, of four and six individuals, respectively, were found, and these were relocated daily with little difficulty. Both occurred in areas of scrub woodland bordering alluvial flats along the upper margins of which were open groves of pine of moderate or small size. In their flights the jays held to the yellow pines, moving over or between them. Sentinel individuals were usually perched high in a pine either when the flock was feeding or when it was slowly moving through the woodland. The more or less continuous scrub woodland of oaks, junipers, piñons intermixed with a variety of other shrubs, agaves, and cacti, present as an association neighboring the pine areas on higher and drier sites, was occupied by *A. coerulescens*. Open groves of pines interspersed with or bordering woodland vegetation were used by *Gymnorhinus*.

Thus the differential species representation at the two localities visited in Arizona and the differences in relative extent of different habitats aided in the recognition of essential habitat components for each species. In the Whiteriver area, at 6,100 feet, no extensive stands of pine of the type occupied by *Cyanocitta* at Sawmill, at 5,600 feet, occurred. Again, scrub woodland such as was present at Whiteriver and *A. coerulescens* were absent at Sawmill, at least at or near the bases of the gentle slopes enclosing a basin area about Sawmill. It is possible that *A. coerulescens* may occur at higher elevations within the Sawmill basin where the vegetation is of lower stature.

In northern Sonora, at Casita, 3,300 feet, in the period from November 6 to 10, 1946, *A. u. arizonae* was common and occurred in flocks of ten to twenty-five. Smaller groups or lone individuals were seen only rarely. Here, as in Arizona, individual flocks, although spending much time roaming through the woodland, did so only locally, and a given flock could be relocated in a certain general area with little difficulty. The jays were observed to feed either on the ground or in peripheral foliage of oaks. They occurred infrequently in open mesquite groves below the main oak zone and in willow groves on adjacent bottom land.

The chief differences between the habitats at the Arizonan and Sonoran localities where *A. u. arizonae* has been observed are the absence, at Casita, Sonora, of at least scattered tall pine trees in the woodland, and the presence of a varied topography of frequent small canyons and draws, often with steep slopes. Conifers such as junipers and piñons probably do not figure critically in the bio-economy of *A. u. arizonae*. This suggestion is based on the facts that in Arizona and Sonora, at least, the Mexican jay is a bird of oak woods and is not known from areas where this Sierra Madran vegetation type is not prominent. The tall pines I consider to be an important component of the habitat of *arizonae*, and their absence at Casita would seem to be compensated for by the varied topography. Thus, sentinel individuals perched atop an oak, of itself a low tree, commanded views downslope and upslope while the other members of the flock fed in small openings somewhere near by and below a sentinel's position. Certain mannerisms of flight among and over pines at Sawmill resembled those such as banking against and swooping along slopes and escaping over ridges at Casita. The implication is that *arizonae*, not a bird given to flying freely in the open, nevertheless requires a vegetation that, at the same time that it affords protection, is open enough at higher levels to permit the direct and strong flights characteristic of this long-winged species. An added implication is that were the terrain at Casita flat and were the woodland monotonous and of low stature, *arizonae* would be less common or absent. This latter point can probably be tested in the field by observation on similar sites.

In summary, *A. ultramarina* occurs chiefly in oak woodlands. Its populations, in the breeding season and for the most part at other times of the year also, are clearly segregated from those of *A. coerulescens* in chaparral and scrub woodland, *C. stelleri* in coniferous woods, and *G. cyanocephalus* in pine-oak parklands or pine-oak woodlands bordering open areas of herbaceous cover. Habitat overlap results for the most part from various transitional forms of the major vegetation types.

Aphelocoma ultramarina wollweberi

Racial characters.—Compared with *arizonae*, under parts lighter; throat dull white (Pallid Mouse Gray); brownish-gray wash of upper chest lighter (Drab Gray—Smoke Gray) and less extensive, but contrasting more with throat and lower breast and belly; shaft streaks obsolescent and confined to upper chest; lower breast, belly, anal area, and under tail coverts white; upper chest overcast with less blue, or blue overcast lacking; back slightly more brown (Hair Brown), overcast with less blue; blue areas slightly darker (Deep Orient Blue—Tyrian Blue on pileum). In size, smaller than *arizonae*; percentage differences in adult males are as follows: wing, -3.1; tail, -5.8; bill length, -7.4; tarsus, -5.0. Wing-tail ratio, 1.160:1. (See table 48 for other statistical data.)

In agreement with van Rossem (1934:453), I find *wollweberi* bluer above and smaller than

arisonae; the pectoral area, although contrasting more with the throat and lower breast than in *arisonae*, as he correctly states, is not, however, darker.

Juvenal plumage: compared with *arisonae*, back more brown (less gray); throat and chest area slightly lighter; otherwise similar in color.

TABLE 48

MEASUREMENTS OF A. U. WOLLWEBER FROM SOUTHWESTERN CHIHUAHUA, SOUTHEASTERN SONORA, SINALOA, AND DURANGO

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	28	153-166	160.9 ±0.7	3.5	2.2
		First-year..	8	150-156	152.8		
	F	Adult.....	22	148-164	155.7 ±0.8	3.7	2.4
		First-year..	9	145-156	151.4		
Tail	M	Adult.....	28	131-149	138.7 ±0.8	4.3	3.1
		First-year..	8	131-140	134.6		
	F	Adult.....	20	128-145	134.6 ±0.9	4.2	3.1
		First-year..	9	125-137	132.1		
Bill length	M	Adult.....	27	17.4-21.7	19.28±0.19	1.01	5.23
	F	Adult.....	21	16.5-20.2	18.20±0.20	0.91	5.01
Bill depth	M	Adult.....	28	8.8-10.2	9.51±0.07	0.35	3.64
	F	Adult.....	19	8.0-9.9	9.18±0.09	0.41	4.42
Bill width	M	Adult.....	28	7.5-9.7	8.65±0.10	0.51	5.92
	F	Adult.....	21	7.7-9.5	8.50±0.10	0.47	5.53
Tarsus	M	Adult.....	27	37.1-43.0	40.14±0.22	1.16	2.90
		First-year..	8	36.6-40.0	38.66		
	F	Adult.....	22	36.8-41.1	39.05±0.28	1.30	3.34
		First-year..	9	37.0-40.5	38.87		
Hind toe	M	Adult.....	28	13.2-15.1	14.32±0.10	0.52	3.62
	F	Adult.....	22	12.4-15.1	13.84±0.18	0.83	6.02
Middle toe	M	Adult.....	28	19.0-21.5	20.01±0.12	0.61	3.06
	F	Adult.....	22	17.2-20.9	19.25±0.19	0.88	4.60
Weights ¹ (gm.)	M	4	84-90	86.5		
	F	3	77-93	87.7		

¹ From southern Durango.

Geographic distribution.—From southeastern Sonora (Rancho Santa Barbara, Mina Abundancia) and southwestern Chihuahua (Bravo, Jesús María, Carmen) south through Sinaloa (Pinos Gordos, Sierra de Choix) and Durango (El Salto, La Boquilla) into western Zacatecas (Valparaíso Mountains, Plateado, Jerez) and immediately bordering parts of northern Jalisco (Colotlán).

The present definition of the range of *wollweberi* is more restricted than that given by Ridgway (1904:342) in that Nayarit (= Tepic) and the greater part of

northern Jalisco are excluded. Ridgway erroneously cited Colonia García under "*wollweberi*" as a locality in southwestern Chihuahua; this locality falls within the range of *arizonae* in northwestern Chihuahua. Western San Luis Potosí is erroneously included in the range of *wollweberi* by Ridgway; Villar, the locality which he lists from that area, is also included by him (1904:340) in the statement of range for the race "*potosina*" (= *sordida*). Hellmayr (1934:56) apparently followed Ridgway and also included western San Luis Potosí in the range of *wollweberi*.

Comparisons.—Among specimens of *wollweberi* available to me, those from northern Durango, including a series of thirteen collected at La Ciénaga de las Vacas at 8,500 feet, best display the color characters of this race. Although moderately worn, they are easily separated from specimens of *arizonae* of comparable wear. Size differences are striking when the largest geographic variants of *arizonae*, those of Gila County (table 42), rather than topotypical specimens are used.

Compared with *gracilis* of Nayarit and northern Jalisco, *wollweberi* is darker and larger. Differences in dorsal coloration correspond to those between *wollweberi* and *arizonae*. (See above.) In *wollweberi*, however, the brownish-gray wash of the upper chest is darker than in *gracilis*; otherwise the under parts of the two races are similar. *Wollweberi* is thus more similar to *gracilis* in color of under parts than to *arizonae*. In dimensions, percentage differences are as follows: wing, +4.6; tail, +5.0; bill length, +11.3; tarsus, +3.8.

The race *wollweberi* of Ridgway (1904:342) and Hellmayr (1934:56) is here divided into two races, for the second of which the name *gracilis* (G. S. Miller, 1896:34), earlier regarded as a synonym of *wollweberi*, is used. Limited material and the proximity of the type localities of *wollweberi* and *gracilis* led Ridgway (*ibid.*) to synonymize *gracilis*. But a series of eleven specimens from the type locality of *gracilis*, Bolaños, together with four from Nayarit, are smaller than those from Zacatecas and are clearly distinguishable on the basis of color as well as size when they are compared with what is here regarded as typical *wollweberi* from northern Durango. The name *gracilis* can thus be applied to the small race of Nayarit. It is very likely that specimens from Bolaños will prove to average slightly larger than those from Nayarit when adequate material becomes available.

Use of the names *gracilis* and *wollweberi* will remain somewhat problematical until adequate series of specimens are available from southern Durango, western Zacatecas, and northern Jalisco. The type locality of *wollweberi* is Zacatecas (Kaup, 1855:1v); in the western part of the state, from present evidence, intergradation occurs between the race occupying mainly southern Chihuahua and Durango and that of Nayarit and north-central Jalisco. The specimens which I have examined from Zacatecas and closely bordering parts of northern Jalisco are more or less intermediate in color between these two races, but in size they are closer to that of Durango. For the greater part of the range ascribed to *wollweberi* by Hellmayr (1934:56) no nomenclatural change is at present necessary. A restricted type locality is desirable and I select the northwesternmost of the Zacatecan localities from which specimens are available, the Valparaíso Mountains, represented by three specimens in the collection of the Biological Survey (Fish and Wildlife Service). It should be emphasized that these do not represent typical *wollweberi*; as

indicated above, specimens from northern Durango best display the characters of that race. (For further discussion of the name *wollweberi* see p. 409.)

Geographic variation and intergradation.—In the Durango population of *A. ultramarina*, geographic trends observed in *arizonae* of Chihuahua reach an extreme in some characters or continue southward into populations of the neighboring race, *gracilis*. Differences between *wollweberi* and *arizonae* in size and in color of under parts (see p. 328) are representative of trends which continue southward.

TABLE 49
MEASUREMENTS OF ADULTS OF *A. U. WOLLWEBERI* FROM ZACATECAS AND
NORTH-CENTRAL JALISCO

	Sex	No of specimens	Range	Mean
Wing	M	5	152 -163	160 0
	F	4	149 -160	156 0
Tail	M	6	127 -141	135 2
	F	4	129 -137	132 5
Bill length	M	6	16 5- 19 0	18 02
	F	4	16 8- 18 6	17 73
Bill depth	M	5	8 9- 10 0	9 56
	F	2	8 2- 9 6	8 90
Bill width	M	6	7 8- 9 1	8 35
	F	4	7 9- 8 8	8 43
Tarsus	M	6	39 8- 40 4	40 38
	F	4	38 4- 40 7	39 96
Hind toe	M	6	13 2- 15 1	14 15
	F	4	13 1- 14 1	13 65
Middle toe	M	6	17 8- 20 2	19 08
	F	4	19 4- 20 3	19 83

But the darker coloration of head and back of *wollweberi* is a distinctive character and serves to separate the Durangan population from duller and paler birds to the south as well as to the north.

Color of under parts of a small percentage of the Durangan specimens suggests *arizonae*. Thus, two (AM 92328, CS 5156) in a series of twenty-three unworn or moderately worn specimens depart from typical *wollweberi* in that the brown wash on the breast of each is slightly darker than average. Throat coloration of three (AM 92328, CM 15985, BS 163995) differs from all others in that it is light dull gray with an asymmetric area of white; on all remaining specimens, however, at least the upper throat or "chin" is white.

Intergradation with both *arizonae* northward and *gracilis* southward along the Sierra Madre Occidental is gradual. Specimens from southern Chihuahua, south-

eastern Sonora, and northeastern Sinaloa are intergrades of varying degree. In size they do not differ from Durangan birds. In color of under parts, occasional variants suggest *arizonae* in that the brownish wash over the breast is more extensive than in *wollweberi* (MCZ 223410, Mina Abundancia). Throat color includes at least a moderate amount of white in all specimens, but intergradation is evident in that the throats of certain fresh-plumaged specimens are entirely white (CAS 42312), and others are light gray with asymmetric areas of white, generally larger than in *arizonae* (e.g., BS 164247, 164249). Color of upper parts averages slightly lighter than typical *wollweberi*; in this character a few specimens do not differ from *arizonae* (e.g., BS 164247-9, CAS 42320, 42321).

Southward, intergradation with *gracilis* is evident in specimens from southern Durango, Zacatecas, and immediately bordering parts of Jalisco. In dorsal coloration they are more or less intermediate between *wollweberi* and *gracilis*. Certain individuals approach *gracilis* closely (e.g., BS 157228, Sierra Madre, Zacatecas); others are more similar to *wollweberi* and distinctly brighter than *gracilis* or *arizonae* (specimens from the Valparaíso Mountains and Florencio). In color of under parts, specimens from this area of intergradation are more similar to *wollweberi*. In size they are generally smaller than typical *wollweberi* and thus approach *gracilis* (fig. 14), but in all dimensions except those of tail length and bill width they are closer to *wollweberi* than to *gracilis*.

A puzzling character of six specimens from southwestern Zacatecas and immediately neighboring parts of Jalisco (Plateado, Florencio, and Colotlán) is the development of a pectoral collar with a moderate but more or less consistent amount of blue overcast and a fairly distinct posterior margin. That this may be more than a matter of individual variation is suggested by a juvenile from the same region (BS 157230, Monte Escobedo), the broad pectoral band of which is darker and more contrasting than that of any specimen of *wollweberi* to the north.

Ecologic distribution.—No data are available other than brief statements that *wollweberi* occurs in pine and oak woodlands (Bailey and Conover, 1935:422; van Rossem, 1945:173).⁴

Aphelocoma ultramarina gracilis

Racial characters.—Compared with *arizonae*, under parts lighter; chest washed with pallid brownish gray, with a barely detectable blue overcast or none at all; remaining under parts white; back washed with less blue, thus slightly darker (Mouse Gray—Hair Brown); blue areas similar. In size, strikingly smaller than *arizonae*; percentage differences in adult males are as follows: wing, -7.6; tail, -10.4; bill length, -17.3; tarsus, -8.6. Wing-tail ratio, 1.162:1. (See table 50 for other statistical data.)

No juvenal specimens have been seen.

Geographic distribution.—Northern Jalisco (Bolaños) and Nayarit (= Tepic) (Santa Teresa and R[ancho?] de Buenavista, Sierra de Nayarit). *Gracilis* is separated geographically from *colimae* of northwestern Jalisco and a population in central Jalisco (see p. 346) by lowlands along the Río Santiago and Río Ameca. Between these two rivers in southern Nayarit lies a mountain mass which is of

⁴ A. u. *wollweberi* was observed and collected in open pine-oak woodland at approximately twenty-two miles west-southwest of Durango, 7,500 feet, Durango, on March 20, 1950. The habitat here resembled woodland frequented by the Mexican jay in Arizona.

particular interest if it is inhabited by *A. ultramarina*, since it is located between the known ranges of *gracilis* and *colimae*. To my knowledge there are no specimens available from this area.

Comparisons.—For a comparison of *gracilis* and *wollweberi* see page 330.

Compared with two specimens from central interior Jalisco, subspecifically indeterminate at present (see p. 346), *gracilis* is slightly lighter and duller in coloration

TABLE 50
MEASUREMENTS OF ADULTS OF *A. U. GRACILIS*

	Sex	No. of specimens	Range	Mean
Wing	M	5	151–156	153.4
	F	7	147–154	149.7
Tail	M	5	127–136	132.0
	F	7	124–134	128.4
Bill length	M	6	15.6–18.6	17.23
	F	7	15.9–17.5	16.73
Bill depth	M	6	8.0–9.2	8.65
	F	7	8.2–9.1	8.69
Bill width	M	6	7.9–8.5	8.25
	F	7	7.5–8.7	7.94
Tarsus	M	6	37.7–39.4	38.60
	F	7	36.8–39.1	37.87
Hind toe	M	6	12.5–13.7	13.08
	F	7	12.3–13.1	12.70
Middle toe	M	6	18.0–19.6	18.63
	F	7	16.9–18.9	17.81

and is smaller. Blue areas of *gracilis* are of a less intense shade, that is, more grayish; in both, however, the pileum is closest to Deep Orient Blue. The back is overcast with less blue; the chest is washed with less dull brownish gray. In dimensions, percentage differences between the averages of five adult males (table 50) and the single adult from central Jalisco (see p. 346) are as follows: wing, –4.7; tail, –5.0; bill length, –8.8; tarsus, –6.8. I judge the latter specimen to be a male; were it a female, the differences between the population of central Jalisco and *gracilis* would prove to be greater.

Compared with *colimae* of central and southern Jalisco, *gracilis* is lighter and smaller. Blue areas are duller and grayer; the back is more gray and overcast with less blue; the chest is washed with less dull brownish gray. In dimensions, percentage differences between *colimae* (table 57) and *gracilis* (table 50) are as follows: wing, –13.0; tail, –17.8; bill length, –7.2; bill depth, –14.5; tarsus, –9.7.

Geographic variation and intergradation.—Only four specimens of *gracilis* are available from Nayarit. On two males (BS 157226, 157227) undergoing the complete molt, areas of fresh plumage on the crown are Deep Orient Blue or Deep Orient Blue—Parula Blue. Two remaining adults, one female (AM 501135) and a specimen marked “♂” but almost certainly a female (AM 501134), are both appreciably duller (pileum Parula Blue—Cadet Gray) than adult females from northern Durango in a comparable stage of wear (AM 92310, Deep Orient Blue—Parula Blue; AM 92323, Deep Orient Blue—Delft Blue). The third and fourth Nayarit specimens, obtained at a locality possibly to the west of that of the first and second specimens, suggest that when adequate series of specimens are available from that state, *gracilis* may prove to be duller and lighter in color than *arizonae*. In this respect and also in lightness of ventral coloration it would thus represent an extreme among all races of *A. ultramarina*.

Intergradation between *gracilis* and *wollweberi* has been discussed (p. 332). Since the type locality of *gracilis* is close to the major area of intergradation, some evidence of trends toward *wollweberi* is to be expected among topotypical specimens. For example, on one adult male (BS 157239) dorsal coloration is slightly darker and the pectoral band is more distinct than in remaining specimens of *gracilis*. Although these differences may fall within the range of individual variation of these characters, it is necessary to emphasize that Jalisco specimens probably do not “typify” *gracilis*.

Intergradation between *gracilis* and populations in interior central Jalisco may occur directly, but this remains to be determined by exploration and collecting over areas from which no specimens are available at present. Between *gracilis* and *colmae* to the south, no intergradation occurs.

Ecologic distribution.—No data are available.

THE “SORDIDA” GROUP OF RACES *Aphelocoma ultramarina couchii*

Racial characters.—Compared with *arizonae*, darker dorsally; pileum, hind neck, and sides of neck darker and more intense blue (Vanderpoel's Blue—Jay Blue); suborbital, subauricular, and auricular regions only slightly darker than pileum, entire side of head being more blue than in *arizonae*; back darker (Hair Brown or Hair Brown—Chaetura Drab), overcast with darker blue; contrast between hind neck and back sharper; throat lighter (dull white), contrasting more strongly with brownish gray of breast; lower breast and belly washed with less brownish gray; upper breast overcast variably with slightly darker blue; shaft streaks absent on breast; ankle feathers darker (Mouse Gray), overcast with dull blue in *couchii* but not in *arizonae*; wings and tail darker (Deep Orient Blue—Tyrian Blue); bill similar in form. In size, smaller than *arizonae*; percentage differences in adult males are as follows: wing, -7.4; tail, -8.6; bill length, -7.2; tarsus, -5.3. Wing-tail ratio, 1.142:1. (See table 51 for other statistical data.)

Juvenal plumage: compared with *arizonae*, darker dorsally; back more brown (Hair Brown), less gray; wings and tail darker (Deep Orient Blue—Tyrian Blue); under parts similar, but throat lighter; bill of fully grown juveniles black or almost so, not light-colored.

Measurements of *couchii* given by Van Tyne and Sutton (1937:60) are based on first-year as well as adult birds; their averages do not differ significantly from those given for adults in table 51, however, because of the preponderance of adults in their sample.

Individual, sex, and age variation.—Color of under parts is more uniform in *couchii* than in *arizonae*. The chief individual difference is in quantity of brownish-

TABLE 51
MEASUREMENTS OF A. U. COUCHII FROM CHISOS MOUNTAINS, TEXAS

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	35	148-159	153.8 ±0.5	2.9	1.9
		First-year..	17	139-151	145.1 ±0.8	3.2	2.2
	F	Adult.....	18	146-155	149.5 ±0.6	2.4	1.6
		First-year..	14	138-150	144.1		
Tail	M	Adult.....	34	127-142	134.7 ±0.6	3.7	2.8
		First-year..	17	122-138	127.9 ±1.1	4.4	3.4
	F	Adult.....	18	125-139	131.4 ±0.9	3.7	2.8
		First-year..	14	113-131	125.2		
Bill length	M	Adult.....	33	16.9-22.0	19.32±0.19	1.08	5.57
		First-year..	15	17.9-21.0	18.86±0.19	0.73	3.85
	F	Adult.....	18	17.4-19.8	18.36±0.16	0.68	3.65
		First-year..	13	16.3-20.2	18.49		
Bill depth	M	Adult.....	32	8.7-10.1	9.51±0.07	0.38	4.02
		First-year..	16	8.6-9.9	9.21±0.08	0.33	3.54
	F	Adult.....	15	8.3-9.6	9.16±0.09	0.36	3.89
		First-year..	13	8.0-9.5	8.97		
Bill width	M	Adult.....	34	8.2-9.8	8.98±0.07	0.42	4.67
		First-year..	16	8.4-9.5	8.84±0.07	0.28	3.15
	F	Adult.....	18	7.8-10.0	8.87±0.12	0.49	5.53
		First-year..	13	7.5-9.3	8.79		
Tarsus	M	Adult.....	35	38.5-42.5	39.99±0.15	0.92	2.29
		First-year..	17	38.2-42.2	40.20±0.27	1.10	2.72
	F	Adult.....	18	37.0-41.7	39.18±0.31	1.30	3.33
		First-year..	14	36.1-40.6	39.26		
Hind toe	M	Adult.....	35	12.9-15.1	13.93±0.08	0.48	3.47
		First-year..	17	12.5-14.7	13.68±0.14	0.56	4.08
	F	Adult.....	18	12.6-14.5	13.62±0.11	0.46	3.35
		First-year..	14	13.0-14.2	13.66		
Middle toe	M	Adult.....	35	18.2-20.7	19.33±0.11	0.64	3.29
		First-year..	17	17.5-19.7	18.61±0.15	0.61	3.26
	F	Adult.....	18	17.5-19.6	18.63±0.13	0.54	2.92
		First-year..	14	17.9-19.1	18.40		
Weights ¹ (gm.)	M	3	99-107	102.7		
	F	3	91-100	98.0		

¹ Reported by Van Tyne and Sutton (1937:60).

gray wash over breast and belly; a few specimens (e.g., MCZ 320117, 320123) are lighter than the majority, the brownish-gray wash being confined to the area of the broad, indistinct pectoral band. Dorsally a slight variation in quantity of blue overcast on the back is evident among individuals. Blue coloration is uniform, the

only notable variants being a few which are slightly lighter than the majority (pileum Vanderpoel's Blue, MCZ 320125).

Sex and age variation in *couchii* is comparable to that in *arizonae*. One notable exception in age variation is the fact that in *couchii* the bill becomes black before the postjuvenal molt is completed, whereas in *arizonae* the bill darkens gradually

TABLE 52

MEASUREMENTS OF *A. U. COUCHII* FROM SOUTHERN COAHUILA AND WEST-CENTRAL NUEVO LEÓN

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult	18	150-161	156.9 \pm 0.8	3.5	2.2
		First-year..	6	146-156	150.0		
	F	Adult.	8	145-158	151.6		
		First-year..	4	142-152	143.7		
Tail	M	Adult.	18	127-143	135.9 \pm 1.1	4.3	3.1
		First-year..	6	126-136	129.8		
	F	Adult.	8	124-137	132.0		
		First-year..	4	121-135	126.7		
Bill length	M	Adult.	17	17.4-20.6	19.26 \pm 0.24	0.99	5.15
	F	Adult.	8	17.9-20.1	19.00		
Bill depth	M	Adult.	15	8.9-10.4	9.72 \pm 0.10	0.40	4.16
	F	Adult.	7	9.0-10.1	9.60		
Bill width	M	Adult.	18	8.5-10.0	8.92 \pm 0.08	0.34	3.82
	F	Adult.	8	8.5-9.4	8.75		
Tarsus	M	Adult.	18	38.5-43.9	41.27 \pm 0.31	1.30	3.15
	F	Adult.	8	38.5-42.4	40.50		
Hind toe	M	Adult.	18	13.5-15.3	14.42 \pm 0.12	0.50	3.47
	F	Adult.	8	13.1-14.8	14.31		
Middle toe	M	Adult.	17	19.5-21.9	20.73 \pm 0.19	0.79	3.80
	F	Adult.	8	18.5-21.2	19.91		
Weights (gm.)	M	4	118-137	125.7		
	F	4	113-127	120.7		

over a period of less than one to more than two years. (See p. 317.) The duller blue coloration of adult females is closest to Vanderpoel's Blue—Deep Orient Blue in variants (MCZ 320138) which differ most strongly from adult males; among first-year females the duller extremes reach Deep Orient Blue—Jay Blue (MCZ 320137).

Geographic distribution.—Mountains of extreme southwestern Texas and north-eastern México, from the Chisos Mountains in Brewster County southeastward through Coahuila to southern Nuevo León (Carneros) and west-central Tamaulipas (Carricitos, Ciudad Victoria, and Miquihuana), and probably northeastern Zaca-

tecas and northern San Luis Potosí. The geographic limits here ascribed to *couchii* include all parts of the Mexican states of Coahuila, Nuevo León, and Tamaulipas in which *A. ultramarina* is known to occur; they are thus more inclusive than those given by Ridgway (1904:342) or Hellmayr (1934:56).

TABLE 53

MEASUREMENTS OF *A. U. COUCHII* FROM SOUTHERN NUEVO LEÓN AND WEST-CENTRAL TAMAULIPAS

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	21	154-165	153.8 ±0.8	3.5	2.2
		First-year..	5	152-159	153.8		
	F	Adult.....	13	147-160	154.5		
Tail	M	Adult.....	20	128-149	138.4 ±1.3	5.6	4.1
		First-year..	4	133-142	137.8		
	F	Adult.....	13	124-140	133.8		
Bill length	M	Adult.....	22	18.0-20.4	19.22±0.15	0.68	3.55
	F	Adult.....	13	17.0-20.9	18.78		
Bill depth	M	Adult.....	21	9.2-11.1	9.81±0.10	0.44	4.46
	F	Adult.....	12	9.0-10.2	9.57		
Bill width	M	Adult.....	22	8.0-10.0	9.18±0.10	0.46	5.02
	F	Adult.....	13	8.4-9.6	9.04		
Tarsus	M	Adult.....	22	39.1-43.2	41.25±0.21	0.98	2.38
	F	Adult.....	11	40.3-42.2	40.99		
Hind toe	M	Adult.....	22	13.6-15.8	14.37±0.12	0.56	3.92
	F	Adult.....	13	13.6-15.3	14.37		
Middle toe	M	Adult.....	22	19.2-21.5	20.43±0.12	0.58	2.86
	F	Adult.....	12	19.4-21.3	19.98		
Weights (gm.)	M	2	102-107	104.3		
	F	2	91-99	95.3		

A female collected at five miles west of Alpine, in northern Brewster County, Texas, on March 25, 1935 (Van Tyne and Sutton, 1937:60), is the only known record of extralimital occurrences of this race. The specimen is not an adult but a first-year bird. It is probable that in this species, as in *A. coerulescens*, there is a tendency for first-year individuals to wander more widely than those which have bred at least once. (See also p. 322.)

A. u. couchii is separated from *A. u. arizonae* to the west by approximately 175 miles of scrub desert in eastern Chihuahua. Its northern limits of occurrence in southwestern Texas form the tip of the eastern arm of a roughly U-shaped geographic range of the species as a whole. (See fig. 13.)

Variation and intergradation.—For a discussion of intraracial variation in *couchii* and of intergradation with *sordida* to the south, see page 339.

Ecologic distribution.—Apparently *couchii* characteristically inhabits the open forests of pines and oaks of the Chisos Mountains and those of the ranges to the south in Nuevo León and Coahuila (Van Tyne and Sutton, 1937:60; Sutton and Burleigh, 1939a:35; Burleigh and Lowery, 1942:196). Nests have been found in oaks, pines, and junipers (Van Tyne and Sutton, *op. cit.*; Burleigh and Lowery, *op. cit.*). In the Chisos Mountains, Van Tyne and Sutton found *couchii* to occur from the lower limit of trees at 5,000 feet upward; they do not record the scrub jay from that locality, although the species presumably occurs there. (See p. 282.) In the Chisos Mountains, *couchii* occurs in groves of live oaks as well as in deciduous oaks, but to the south, in Nuevo León, live-oak groves are found at elevations below those of the mountain forests of pine and oak occupied by *couchii*, and the live-oak groves are occupied by *Xanthoura* (Sutton and Burleigh, 1939b:174). In Nuevo León, *A. u. couchii* occurs as low as 2,000 feet on the Mesa del Chipinque, near Monterrey (Sutton and Burleigh, 1939a:35), an area from which *A. coerulescens* has not been recorded. East of Galeana, in late February, but probably not in the breeding season, *couchii* ranges down to the base of the foothills (Sutton and Pettingill, 1943:282). In southern Coahuila, however, *couchii* has not been recorded below 6,500 feet (Sutton and Burleigh, 1942:196), and its main altitudinal range is above that of *A. coerulescens*. These scant data merely provoke many fundamental questions on the ecologic interrelationships of the two species of *Aphelocoma* as well as other jays found in northeastern Mexico.

Aphelocoma ultramarina sordida

Racial characters.—Compared with *couchii*, darker; average shade of blue on head, wings, and tail slightly more intense (pileum Jay Blue); back overcast with slightly more blue; bill less pointed. In size, larger than *couchii*; percentage differences in adult males are as follows: wing, +6.8; tail, +8.6; bill length, +2.2; tarsus, +5.4. Wing-tail ratio, 1.123:1. (See table 54 for other statistical data.)

According to Nelson (1899a:28), "*potosina*" (= *sordida*) differs from *couchii* in size and in the following color characters: the back is more bluish and the under parts are grayer. Individual variation in both of these characters is such that in the first instance the difference is evident only when series are compared, and in the second instance no consistent difference can be seen. The chief differences, then, are in size.

No juvenal specimens have been seen. First-year specimens indicate that the bill becomes black before the postjuvenal molt is completed, as in *couchii*.

Geographic distribution.—East-central México, from San Luis Potosí (Villar) south to central Hidalgo (El Chico). This race is stated to occur in eastern Zacatecas, Guanajuato, and northern Querétaro (Nelson, 1899a:27), but to my knowledge there are no published records from these areas other than Duges' (1870:139) mention of "*Cyanocitta sordida*" as occurring in Guanajuato. The Museum of Vertebrate Zoölogy has recently received specimens of this race collected at Amoles, Querétaro. Southern Coahuila, western Tamaulipas, and southeastern Hidalgo (Ridgway, 1904:340; Hellmayr, 1934:57) are here excluded from the range of *sordida*.

Comparisons.—Compared with *ultramarina* to the south, *sordida* is duller, and smaller in all dimensions except those of the bill. Color differences parallel those

between *ultramarina* and *couchii*. (See p. 341.) Differences in average dimensions, expressed as percentage, are as follows: wing, -9.0; tail, -12.9; bill length, +6.6; tarsus, -3.2.

Compared with *wollweberi* to the west (table 49), *sordida* is darker and slightly

TABLE 54
MEASUREMENTS OF A. U. SORDIDA

	Sex	Age group	No. of specimens	Range	Mean
Wing	M	Adult.....	7	157 -172	164.3
		First-year.....	4	147 -160	153.3
	F	Adult.....	5	156 -161	157.8
		First-year.....	2	150 -151	150.5
Tail	M	Adult.....	6	136 -151	146.3
		First-year.....	4	126 -138	133.0
	F	Adult.....	5	134 -143	138.4
		First-year.....	2	129 -130	129.5
Bill length	M	Adult.....	7	17.8- 22.0	19.74
	F	Adult.....	5	18.6- 20.0	19.30
Bill depth	M	Adult.....	7	8.9- 10.5	9.81
	F	Adult.....	5	9.1- 10.3	9.78
Bill width	M	Adult.....	7	8.6- 9.6	9.04
	F	Adult.....	5	8.1- 9.6	8.96
Tarsus	M	Adult.....	7	40.9- 43.9	42.16
	F	Adult.....	5	40.1- 42.2	40.98
Hind toe	M	Adult.....	6	14.0- 15.3	14.63
	F	Adult.....	5	13.7- 14.7	14.28
Middle toe	M	Adult.....	7	19.8- 21.6	20.67
	F	Adult.....	5	18.2- 20.5	19.80
Weights (gm.)	M	2	129 -137	133.0
	F	2	120 -132	126.0

larger. Differences in average dimensions, expressed as percentage, are as follows: wing, +3.1; tail, +10.3; bill length, +7.8; tarsus, +5.3.

Geographic variation and intergradation.—There is little evidence of geographic variation in color over the combined ranges of *couchii* and *sordida*. Color differences described above would indicate that from typical *couchii* in southwestern Texas to typical *sordida* in San Luis Potosí (or Hidalgo?) there is apparently a trend toward darker blue coloration and increased overcast of blue on the back. More striking, however, is a size cline from a small extreme in the Chisos Mountains to a large extreme in San Luis Potosí and northern Hidalgo. Intergradation be-

tween them is gradual. Although specimens from southern Coahuila, central and southern Nuevo León, and Tamaulipas are intergrades in varying degrees, samples from these areas available to me prove to be closer to *couchii* than to *sordida* in average measurements (fig. 14). Certain specimens from southern Tamaulipas, considered individually, are not distinguishable from *sordida*, but from the standpoint of a series of specimens considered as a whole, all are more properly placed with *couchii*.

The relationships of *sordida* and *ultramarina* in Hidalgo are not clearly understood at present. (For explanation of the use of the name *sordida* in place of *potosina* see p. 412.) Whereas intergradation between *sordida* and *couchii* is gradual, that between *sordida* and *ultramarina*, if it actually occurs to any appreciable extent, is apparently abrupt. Specimens from northern and central Hidalgo are not distinguishable from those of San Luis Potosí in size or color. *A. u. sordida* and *A. u. ultramarina* meet in southern Hidalgo. The few specimens from the latter area are of particular interest because they were assigned to "*potosina*" (= *sordida*) by Ridgway (1904:340). Hellmayr (1934:57) apparently followed Ridgway and on the basis of the type locality, Real del Monte, of Swainson's *Garrulus sordidus*, replaced Nelson's name, *potosina*, with *sordida*. Two specimens from Tulancingo are juveniles in early stages of postjuvinal molt, and one specimen from El Chico is an adult male. Wing and tail measurements of these three birds are 170, 173, 172, and 155, 155, 159 mm., respectively. The juveniles are clearly out of the range of first-year specimens of *sordida* (table 54), among which the wing of the largest specimen measures 160 mm. The single adult is slightly smaller than any available adult male of *ultramarina* and is of the same size as the largest adult male of *sordida*.

I have seen no juvenal specimens of typical *sordida*, but on the basis of the similarities between adults of *sordida* and of *couchii* which almost certainly obtain in the juvenal plumage as well, the two Hidalgo specimens may be compared with juveniles of *couchii* and *ultramarina*. They prove to be similar to those of the latter race. Moreover, a small area of fresh blue plumage on the head of one is darker (more purplish) than the crown color of a first-year male from northern Hidalgo and is similar to the crown color of first-year birds of *ultramarina*. Flight feathers are slightly less purplish than, or similar to, those of juvenal or first-year specimens of *ultramarina* from Veracruz, and thus are more purplish than those of first-year specimens from northern Hidalgo. The adult specimen from El Chico, however, does not differ in color from comparably worn specimens of *sordida*. Its large size suggests intergradation with *ultramarina*; it is only slightly smaller than the supposed type of *Garrulus sordidus* Swainson (1827:437) according to the measurements of van Rossem. (See p. 412.) Swainson's type may have been obtained at Real del Monte not far southeast of El Chico. It is doubtful whether specimens from El Chico and Real del Monte differ significantly, since both localities are in a more interior, drier part of the Sierra Madre than is Tulancingo.

Thus, on the basis of the evidence provided by the two juvenal specimens, the southeastern part of Hidalgo is occupied not by *sordida* (see p. 338) but by *ultramarina*. South-central Hidalgo is here placed in the range of *sordida*, but extensive collecting is necessary before the geographic relations of these races can be deter-

mined satisfactorily.⁵ Nothing is known of their relations in northern Mexico, southern Querétaro, and southwestern Hidalgo.

According to Nelson (1899:28), *sordida* intergrades westwardly through Zacatecas with "*gracilis*" (= *wollweberi* of this paper), but I have seen only suggestive evidence of this. Specimens from western Zacatecas are all lighter and smaller than typical *sordida* and are placed with *wollweberi*. I have seen no specimens from central or eastern Zacatecas, and am aware of but one record from a locality bordering these areas on the west, that of G. S. Miller (1896:37) of an adult male, taken at Jerez, which he includes among specimens of *Aphelocoma couchii*.⁶ Of the latter he states (p. 35) that "none . . . are near enough to *A. gracilis*, either in size or color, to cause any difficulty in distinguishing the two birds. The blue on the head, wings, tail, and upper tail-coverts is darker and much more intense in *A. couchii* than in *A. gracilis*." These remarks would indicate that the Jerez specimen is closer to *sordida* in color than to *wollweberi* of western Zacatecas, but judging by the geographic position of Jerez this would seem doubtful. I have recently examined this specimen (BM 1906:12:7:3716) and find that it does not resemble *sordida*. In size the Jerez specimen (wing, 163 mm.) approximates the largest specimen from western Zacatecas. In color it is clearly similar to, although slightly brighter than, *gracilis*. Blue areas of this specimen are somewhat more intense (less gray) than those of topotypes of *gracilis*, but they are still closest to Deep Orient Blue. In color the Jerez specimen resembles others in comparable plumage from western Zacatecas; it is virtually identical with an adult male from Florencio (BS 157244). Determination of the relationships of *sordida* and *wollweberi* must await collection of adequate series of specimens; the separation of these races in Zacatecas must rest primarily on color characters, for there is considerable overlap in all dimensions (fig. 14).

Ecologic distribution.—According to Nelson (1899a:27), *sordida* inhabits pine and oak forests on mountains of the east-central part of the Mexican tableland.

THE "ULTRAMARINA" GROUP OF RACES

Aphelocoma ultramarina ultramarina

Racial characters.—Compared with *couchii*, darker; blue areas more purplish (pileum Eton Blue); back darker, ground color (Fuscous—Hair Brown) overcast with blue, comparable in amount but more purplish; light brownish-gray wash over upper chest slightly darker; bill slightly shorter and less pointed; thus, culmen more abruptly curved distally, curvature of gonys greater, and hook more prominent. In size, larger than *couchii*; percentage differences in adult males are as follows: wing, +17.4; tail, +24.7; bill length, -4.1; tarsus, +8.9. Wing-tail ratio, 1.075:1. (See table 55 for other statistical data.)

The difference in bill size evident from the comparison of dimensions is somewhat exaggerated, owing to the fact that *couchii* and *ultramarina* differ not so much in actual length as in the

⁵ An important specimen bearing on this point is one I examined at the Instituto de Biología, Mexico City, in March, 1950, through the courtesy of Rafael Martín del Campo. It is a juvenile female from the "Sierra de Pachuca," collected June 10, 1934, by M. del Toro Avilés, and represents *A. u. ultramarina* (wing, 158 mm.; tail, 141 mm., but central pair of rectrices still sheathed basally; tarsus, 41 mm.; base of mandible yellow). If the specimen comes from the restricted mountain mass in which Pachuca, Real del Monte, and El Chico are located, then this is the first evidence of the presence of the "race" *ultramarina* in an area from which all previously collected specimens represent *A. u. sordida*. The suspicion, elsewhere expressed, that the striking morphological gap between *sordida* and *ultramarina* suggests a secondary contact, if not a break at the species level, is thus supported.

⁶ See also Nelson (1899a:27).

position of the nostrils. The nostrils of *ultramarina* are larger, and the peripheral excavation of the upper mandible is more gradual, tending in most specimens to form a short, shallow trough anterior to the nostril. As a consequence, the front margin of the nostril is closer to the tip in *ultramarina* than in *couchii*, and the bill of *ultramarina* is heavier basally than the figures of table 55 indicate. Viewed in the light of comparative body sizes, *ultramarina* has an appreciably smaller bill than *couchii*.

TABLE 55
MEASUREMENTS OF ADULTS OF *A. U. ULTRAMARINA* FROM VERACRUZ, PUEBLA, MORELOS,
AND MÉXICO

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	17	175-187	180.6 \pm 0.9	3.8	2.1
	F	9	169-182	173.7		
Tail	M	17	161-182	168.0 \pm 1.3	5.4	3.2
	F	10	155-171	160.9		
Bill length	M	17	16.6-20.0	18.52 \pm 0.21	0.85	4.58
	F	10	17.8-18.8	18.25		
Bill depth	M	17	8.2-10.2	9.66 \pm 0.11	0.47	4.85
	F	7	8.2-10.2	9.68		
Bill width	M	17	7.7-10.3	8.84 \pm 0.15	0.63	7.16
	F	10	8.4-10.2	9.23		
Tarsus	M	17	42.1-44.9	43.56 \pm 0.19	0.80	1.84
	F	10	40.8-43.5	42.29		
Hind toe	M	16	14.1-15.5	14.94 \pm 0.10	0.40	2.67
	F	10	14.1-15.2	14.58		
Middle toe	M	17	20.0-22.2	21.12 \pm 0.15	0.61	2.87
	F	10	19.3-21.1	20.35		
Weights ¹ (gm.)	M	4	123-135	130.5		
	F	2	129-131	130.0		

¹ Two records used reported by Davis (1945: 279).

Juvenal plumage: compared with *couchii*, darker dorsally; back browner (Fuscous), thus less gray; wings and tail darker and brighter (Ochapman's Blue—Tyrian Blue); upper breast darker (Drab to Hair Brown), broad pectoral band thus more distinct; basal half of mandible and of maxillary tomium light-colored (yellow in dried specimens, flesh-colored in life), bill thus not entirely black or blackish.

Geographic distribution.—Southern part of the Mexican plateau, from Veracruz (Jalapa, Mirador) west through southeastern Hidalgo (Tulancingo), Tlaxcala, northern Morelos (Tetela del Volcán), and México, to northwestern Michoacán (Patambaro, Tanicítaro) and southeastern Jalisco (Cerro García, 32 mi. S Guadalupe).

The range ascribed here to *ultramarina* differs from that of Ridgway (1904:338) and Hellmayr (1934:58) only in that southeastern Hidalgo is included.

Comparisons.—For a comparison of *ultramarina* and *sordida* see page 338.

Compared with *colimae*, *ultramarina* is darker. Blue areas are more purplish; the back is more brown and suffused with more blue; the under parts are washed with more dull brownish gray, the pectoral area being darker. *Ultramarina* is larger

TABLE 56
MEASUREMENTS OF ADULTS OF A. U. ULTRAMARINA FROM MICHOACÁN

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	16	171–183	175.9 ±0.9	3.5	2.0
	F	11	165–180	172.2		
Tail	M	12	153–173	162.1		
	F	10	152–168	158.6		
Bill length	M	15	17.7–20.5	18.98±0.22	0.87	4.58
	F	13	18.7–21.1	18.72		
Bill depth	M	13	9.7–11.0	10.36		
	F	9	9.7–10.6	10.21		
Bill width	M	15	8.5–10.2	9.46±0.13	0.50	5.26
	F	13	9.0–10.1	9.43		
Tarsus	M	16	41.2–44.3	42.91±0.24	0.95	2.21
	F	13	40.2–43.8	42.22		
Hind toe	M	16	14.2–15.6	14.87±0.10	0.41	2.77
	F	13	13.9–15.6	14.79		
Middle toe	M	16	20.0–22.0	21.10±0.14	0.54	2.56
	F	13	20.0–21.9	21.19		
Weights (gm.)	M	8	134–150	140.6		
	F	2	125–137	131.0		

than *colimae* in all dimensions except those of the bill; differences, expressed in percentage, are as follows: wing, +2.4; tail, +4.5; bill length, –3.0; tarsus, +1.9.

Variation and intergradation.—For a discussion of the geographic relations of *ultramarina* and *sordida* see page 340.

A. u. ultramarina apparently intergrades gradually with *colimae* through Michoacán. In color the series of specimens from this state available to me is less purplish than a series from Veracruz and Puebla, but is more similar to the latter than to *colimae* of the Sierra Nevada de Colima. In average dimensions (table 56), however, the Michoacán specimens are more similar to *colimae* than to *ultramarina* (fig. 14). Since the primary basis for the nomenclatural separation of *ultramarina* and *colimae* is color, the Michoacán population is retained under the name "*sieberi*" or *ultramarina* (Ridgway, 1904:338; Hellmayr, 1934:58).

Two juvenal specimens from Michoacán are more or less intermediate between one juvenile of *ultramarina* from Veracruz and one juvenile of *colimae* from Jalisco in color of flight feathers. They do not appear to differ significantly from the Veracruz specimen in other color characters except that under parts of both are lighter and the pectoral band is more distinct.

From the available evidence it would appear that *ultramarina* of Veracruz and Puebla represents one end of an east-to-west cline; *colimae* of northwestern Jalisco, the other end. The cline from dark to light coloration is apparently steepest in extreme western Michoacán and neighboring parts of Jalisco. In dimensions, wings, tail, and tarsi become shorter from east to west, but the bill becomes longer, and the most sudden change in size apparently occurs in eastern Michoacán and western México.

Ecologic distribution.—In Veracruz and Puebla, *A. ultramarina* is apparently confined to pine forests at elevations of 8,000 to 10,500 feet (Chapman, 1898:42; Davis, 1945:273, 279). It is probable that its restriction to higher elevations in this part of Mexico is due in part to clearing of timber below 8,000 feet. In Michoacán, the distribution of *A. ultramarina* coincides with that of pine forests and extends from 3,000 to 11,000 feet (Blake and Hanson, 1942:537). At lower elevations the predominant pines are *Pinus ayacahuite* and *P. montezumae*; from 4,500 feet to 9,500 feet, conifers are mixed locally with deciduous trees such as oaks, willows, lindens, and alders; above 9,500 feet, *P. montezumae* and *Juniperus mexicanus* predominate. The altitudinal range of *A. ultramarina* includes a belt of cloud forest between 6,000 and 8,500 feet on Cerro de Tancítaro, to which *Cyanocitta stelleri* is restricted.

Aphelocoma ultramarina colimae

Racial characters.—Compared with *couchii*, darker only above; pileum, hind neck, and sides of head and neck more purplish (Eton Blue—Dark Tyrian Blue); blue overcast of back more purplish, but ground color of back similar to that of *couchii* (Hair Brown); under parts lighter, white of anal area extending anteriorly over belly and lower breast, and white of chin area extending over more of throat; upper chest with less dull brownish gray, without any overcast of blue, thus lighter; pectoral band thus more obsolescent than in *couchii* or any member of *ultramarina* group except *gracilis*; ankle feathers lighter (Smoke Gray), without any overcast of blue. In size, larger than *couchii*; percentage differences in adult males are as follows: wing, +14.6; tail, +19.2; bill length, -1.1; tarsus, +6.9. Wing-tail ratio, 1.098:1. (See table 57 for other statistical data.)

Juvenal plumage: only one specimen from Jalisco seen, female (AM 501131) collected northeast of Mascota, May 11, 1892, in early stage of postjuvenal molt; compared with juvenal female of *ultramarina* from Veracruz (USNM 42081), blue areas appreciably less purplish (Tyrian Blue—Deep Orient Blue); brown of head and back slightly duller, that is, more grayish (but still closest to Fuscous); under parts too soiled for appraisal of color characters.

Differences between *couchii* and *colimae* in juvenal plumage parallel those between *couchii* and *ultramarina* (see p. 342) in all characters except color of flight feathers; in *colimae* these are only slightly more purplish (Tyrian Blue—Deep Orient Blue) than in *couchii*.

Geographic distribution.—From northwestern Jalisco (San Sebastián, Sierra de Juanacatlán), southeastward to south-central Jalisco (5 mi. SW Cocula, 6,800 ft.) and northeastern Colima (Sierra Nevada de Colima).

According to Nelson (1899a:27), *colimae* ranges north to the Río Santiago, but it is doubtful if he collected specimens from localities other than those represented

by specimens which I have seen. He probably based his statement of range in part on field observations.

Comparisons.—For a comparison of *colimae* and *ultramarina* see page 343; of *colimae* and *gracilis*, page 333.

TABLE 57
MEASUREMENTS OF A. U. COLIMAE

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	19	167-185	176.3 ±1.0	4.1	2.4
		First-year..	4	165-174	169.0		
	F	Adult.....	20	167-179	173.6 ±0.8	3.4	1.9
Tail	M	Adult.....	19	151-170	160.5 ±1.3	5.6	3.5
		First-year..	3	156-168	157.0		
	F	Adult.....	21	146-168	156.2 ±1.2	5.4	3.4
Bill length	M	Adult.....	18	17.5-20.8	19.10±0.19	0.81	4.25
		First-year..	4	19.0-19.7	19.28		
	F	Adult.....	20	17.8-20.7	18.74±0.19	0.84	4.48
Bill depth	M	Adult.....	14	9.6-11.0	10.12±0.10	0.38	3.71
		First-year..	4	10.0-10.9	10.38		
	F	Adult.....	18	8.3-10.7	10.03±0.13	0.53	5.30
Bill width	M	Adult.....	18	8.4-10.6	9.27±0.13	0.56	6.01
		First-year..	4	9.1-11.0	9.88		
	F	Adult.....	21	8.4-10.2	9.44±0.10	0.46	4.88
Tarsus	M	Adult.....	19	40.2-45.0	42.73±0.27	1.19	2.78
		First-year..	4	40.5-43.5	42.15		
	F	Adult.....	21	39.3-44.9	42.43±0.29	1.33	3.13
Hind toe	M	Adult.....	19	14.2-15.6	15.13±0.10	0.43	2.83
		First-year..	4	14.6-15.8	14.98		
	F	Adult.....	21	14.2-15.8	14.98±0.10	0.44	2.92
Middle toe	M	Adult.....	19	20.0-22.0	21.02±0.15	0.67	3.16
		First-year..	4	20.1-20.9	20.60		
	F	Adult.....	21	19.3-21.8	20.60±0.14	0.62	3.20

Compared with two specimens from interior central Jalisco, unidentified sub-specifically, *colimae* is darker dorsally and larger; blue areas of *colimae* are more purplish and the back is more brown. Percentage differences between average dimensions of adult and first-year males of *colimae* and those of a single adult and a single first-year male from interior Jalisco are given in the table on page 346.

Variation and intergradation.—Intergradation of *colimae* with *ultramarina* eastwardly has been discussed (p. 343). *Colimae* is not known to intergrade with any population in interior Jalisco.

In the series of *colimae* available to me, intraracial variation is suggested by

slight differences in blue coloration. Specimens from northwestern Jalisco are slightly less purplish than others from the Sierra Nevada de Colima. Because the former are worn to varying degree, whereas the latter are in fresh plumage, it is not possible to define the difference precisely. At any rate, these differences are indicative of the east-to-west cline in color (see p. 343) which extends from Vera-

	Adult males	First-year males
Wing.....	+ 8.7	+ 9.5
Tail.....	+13.4	+12.7
Bill length.....	+ 1.0	+ 9.8
Tarsus.....	+ 3.1	+ 4.4

cruz to Jalisco. The population of northwestern Jalisco represents the less purplish, lighter-colored extreme. It may be noted that this population and that of the Sierra Nevada de Colima are about equidistant from the inadequately known, more interior population discussed in the next section.

Ecologic distribution.—According to Nelson (1899a:27), *colimae* occurs in pine and oak forests.

Aphelocoma ultramarina subsp. ?

Racial characters.—Compared with *couchii*, duller and paler (thus contrasting with *colimae* and *ultramarina* and suggesting “*wollweberi*” group of races); pileum, hind neck, and sides of neck of adult (AM 501128, probably a male) Deep Orient Blue; pileum of first-year male (AM 501127) slightly duller than that of adult, but closest to Deep Orient Blue; back of both specimens lighter (grayer) than in *colimae*; under parts of both specimens similar to *colimae*. Dimensions (mm.) of the two specimens are given in the table. In size, the single adult is smaller than all adults of

	Adult (male?) AM 501128 (Oct. 20, 1893)	First-year male AM 501127 (Nov. 4, 1892)
Wing.....	161	153
Tail.....	139	137
Bill length.....	18.9	17.4
Bill depth.....	8.9	9.2
Bill width.....	7.8	8.3
Tarsus.....	41.4	40.3
Hind toe.....	14.3	14.3
Middle toe.....	19.4	19.8

both sexes of *colimae* in lengths of wing and tail, width of bill, and, compared with males only, depth of bill; differences in these dimensions between averages of adult males of *colimae* and the adult listed in the accompanying table are 15.3, 21.5, 1.5, and 1.2 mm., respectively. The first-year male is smaller than available first-year males of *colimae* in lengths of wing and tail and all dimensions of the bill; differences in these dimensions between averages of *colimae* and the first-year male listed in the table are 16.0, 20.0, 1.3, 1.2, and 1.6 mm., respectively. Feet of two indeterminate specimens apparently average slightly smaller than those of *colimae*.

Geographic distribution.—Both specimens were obtained at Tinguindi, a ranch in the municipality of Ixtlahuacán del Río, fifteen miles north-northeast of Guadaluajara, Jalisco.*

* The identity of this puzzling locality was only recently obtained through the kindness of Dr. M. Martínez of the Instituto de Biología, Mexico City, and Dr. C. G. Sibley.

Comparisons.—The specimens from interior Jalisco are compared with *gracilis* on page 333, and with *colimae* on page 345. In size they are apparently intermediate between *colimae* (table 57) and *gracilis* (table 50). Differences between *gracilis* and *colimae* in dimensions are unusually large (see p. 333), there being no overlap in those of wing, tail, and feet; thus the intermediacy of the two problematical specimens does not imply dubious size differences.

The same two specimens fall within the range of variation of most dimensions of *wollweberi* from western Zacatecas and immediately adjoining parts of northern Jalisco (table 49), but both are larger than average specimens of corresponding sex and age of that population. In dorsal coloration they do not differ from *wollweberi* of Zacatecas. Under parts differ in that the Jalisco specimens lack any blue overcast on the upper chest, a character surprisingly developed in the Zacatecan specimens available to me; also, the brownish-gray wash on the upper chest of the former does not suggest a pectoral band, whereas Zacatecan specimens have a comparatively well-defined pectoral band. (See p. 332.) These differences are slight, however, and it would seem that the two Jalisco specimens may be only intergrades between *wollweberi* of Zacatecas and *colimae*. There is little doubt, however, about their distinctness in comparison with *colimae* (see above); it remains to place the birds from central Jalisco with *wollweberi* or to consider them another race. That they may represent a distinct race is supported by the following considerations: specimens from western Zacatecas and immediately adjoining parts of Jalisco, although placed under the name *wollweberi*, do not represent that race in typical form; rather, they are intergrades between *wollweberi* of Durango and *gracilis* of Nayarit and north-central Jalisco. It is even possible that in western Zacatecas there is some influence from the race to the east, *sordida*, and that the specimens may therefore represent three-way intergrades. Thus, although similar to those from central interior Jalisco in a number of characters, the Zacatecan population is a link, either through geographic intergradation or structural intergradation, or both, between typical *wollweberi*, *gracilis*, the Jalisco specimens of uncertain subspecific identity, and possibly *sordida*. A satisfactory understanding of this situation must await further exploration and collecting in southeastern Nayarit, northeastern Jalisco, southern Zacatecas, Aguascalientes, and Guanajuato.⁷

In summary, structural characters peculiar to specimens from interior central Jalisco are pale coloration, which distinguishes that race from *wollweberi*, *sordida*, and *colimae*, and intermediate size, which distinguishes it from the small race *gracilis* and the large race *colimae*. The population represented by the Jalisco specimens is apparently similar in size to typical *wollweberi* and to *sordida*; in color it resembles most closely *wollweberi* of Durango. It may prove best to place the interior Jalisco population under the name *wollweberi* if the supposed differences prove to be weak.

⁷ The tentative conclusion that specimens from interior Jalisco may represent an undescribed race is supported by two specimens obtained in 1950 by O. G. Sibley in southern Nayarit (6 mi. S Ixtlán del Río, 6,800 ft.) and northern interior Jalisco (12 mi. W Yahualica, 8,000 ft.).

VARIATION AND INTERRELATIONSHIPS AMONG RACES OF
APHELOCOMA UNICOLOR

A. unicolor of southern Mexico and Central America consists of five races. Since available specimens of this species total only 203, and since the races are comparatively restricted in range, each account which follows consists only of a description, a statement of geographic range, and comparisons. Geographic variation, ecologic distribution, and nomenclatural history are presented from the standpoint of the species as a whole.

Aphelocoma unicolor unicolor

Description and racial characters. Male: adult fall plumage.—Body plumage and wing coverts more or less uniformly dark blue (Prussian Blue—Hortense Blue); back slightly duller (less blue) than pileum and hind neck, hence appearing slightly more black; lores and postocular area black; chin streaked with dull gray; upper surfaces of remiges and rectrices slightly duller than body plumage, under surfaces brownish black; bill, black and heavy, with short hook and culmen curved more or less sharply terminally; feet, black; iris, brown. Wing longer than tail (ratio, 1.072:1). (For dimensions see table 58.)

Female: adult fall plumage.—Similar to male, but averages slightly less purplish.

Male and female: first-year fall plumage.—Similar to adult except that remiges and rectrices of juvenal plumage are retained through postjuvenal molt, as are greater primary coverts, most and usually all greater secondary coverts, and variable number of middle secondary coverts; blue coloration apparently averages less purplish than in adults of corresponding sex, as in *A. coerulescens*; bill yellow to variable extent; tip and most of upper mandible brown or black, basal part and most of lower mandible yellow; color of latter is gradually replaced by black during first and second years (Pitelka, 1945b:257).

Male and female: juvenal plumage.—Body plumage dull dark brown (Chaetura Drab—Hair Brown); middle coverts and marginals, except those at bend of wing, also dull dark brown, but overcast slightly with dull blue; remiges and rectrices dull dark blue (Indigo Blue); greater coverts similar or slightly duller; under surfaces of remiges and rectrices dull brownish black; bill, tip, and most of upper mandible dark or black, base and most of lower mandible dull yellow (Colonial Buff); feet, blackish brown or black.

Geographic distribution.—Mountains of Chiapas, in southeastern México, and Guatemala, at elevations of 7,000 to 10,000 feet. Recorded as low as 1,200 meters at Barranca Honda, Chiapas (MCZ 273091, an adult male, taken on October 30, 1940), and at 4,000 feet, near Chilasco, Guatemala (Salvin and Godman, 1887:495).

A. u. unicolor is primarily a race of the highlands of western Guatemala, with a range extending into central Chiapas to the vicinity of San Cristóbal, and into southwestern Chiapas northwestward along the Sierra Madre to Pico de Loro. The two tongues are separated by the valley of the Río Grijalva. The lowlands of the Isthmus of Tehuantepec separate *unicolor* from the neighboring race to the northwest, *oaxacae*. Eastward, *unicolor* ranges along a tongue of mountains, the Sierra de las Minas, in the direction of Lake Yzabal, as far as Chilasco (Salvin and Godman, 1887:494). Along the main chain of volcanic mountains paralleling the Pacific coast, *unicolor* is not known southeast of Tecpam, but it probably ranges to the volcanoes Agua and Pacaya. Beyond these the altitude decreases rapidly toward the Salvador frontier (Griscorn, 1932:17). The valley of the Río Montagua and an extensive central area not exceeding 5,000 feet in altitude separate *unicolor* from the race *griscomi* of Honduras and El Salvador.

Comparisons.—See the accounts which follow for a comparison of each race with *unicolor*.

Aphelocoma unicolor oaxacae

Racial characters.—Compared to *unicolor*, darker (more purplish); unworn lateral neck plumage of adult male (see p. 263) Cyanine Blue—Dusky Blue, tending toward Azurite Blue—Indulin Blue; body plumage of adult female (type) slightly less purplish than male, but closest to Cyanine Blue—Dusky Blue. In size, probably averages smaller than *unicolor* in length of tarsus and wing; tail proportionally longer than in *unicolor*, same length as, or slightly longer than, wing. Measurements (mm.) of available specimens are given in the table.

	Adult male (RTM 33382, Totontepec, April 7, 1942)	Adult female (type, RTM 39121, Moctum, Oct. 18, 1941)	Juvenal male ² (BS 144681, Mount Zempoaltepec, July 31, 1894)
Wing.....	156	160	150
Tail.....	157	162	146
Bill length.....	20.2	18 ¹
Bill depth.....	10.6	10.0
Bill width.....	10.5	10.5
Tarsus.....	39.7	39.5	39.0
Hind toe.....	14.2	14.5	13.4
Middle toe.....	20.2	19.5	17.9
Wing-tail ratio.....	0.994:1	0.998:1	1.027:1

¹ Tip broken.

² In early stage of postjuvenal molt.

From a comparison of these data with those for *A. u. unicolor* (table 58) it is evident that the wing of the adult male is shorter than that of any adult male of *unicolor*; the wing of the female is slightly longer than the average wing length of adult females. The tail of the male is longer than the average tail length of adult males of *unicolor*; the tail of the female is longer than that of any adult female of *unicolor*. Both adults of *oaxacae* have shorter tarsi than any specimens of *unicolor*. There is no suggestive evidence of differences in dimensions of the bill. Thus, besides color differences, *oaxacae* would appear to differ from *unicolor* in average length of wing and tarsus and in having a proportionally longer tail. The differences are borne out by comparing dimensions of the juvenal specimen (see table) with those of first-year males of *unicolor* (table 58).³

Juvenal plumage: compared to *unicolor*, one specimen differs distinctly in being darker and more purplish; body plumage Fuscous to Fuscous—Black; back slightly darker than head and under parts, overcast with blue; rectrices, remiges, and greater coverts Nigrosin Blue; bill of a richer yellow (Honey Yellow).

Geographic distribution.—State of Oaxaca, southern Mexico; known only from three specimens for which locality data are given above. Du Bus (1848) reported "*Cyanocorax unicolor*" from Tepitongo and San Pedro, an unidentifiable locality, in Oaxaca. Thus, so far as known, *oaxacae* is confined to the central highlands of Oaxaca and is separated from both *unicolor* to the east and *guerrerensis* to the west by approximately 200 miles and from *concolor* to the northwest by approximately 100 miles. Ridgway (1904) for some reason did not mention Oaxaca in his statements concerning the known distribution of *A. unicolor*, although there was a specimen in the collections in Washington, D.C., obtained by Nelson and Goldman

³ Measurements from thirty-six additional specimens in the Moore Collection, Pasadena, kindly provided by B. T. Moore and John Davis, confirm the differences predicted above. For 13 adult males, the average measurements are as follows (mm.): wing, 157.5; tail, 159.3; bill length, 20.63; bill depth, 10.42; tarsus, 40.68; hind toe, 14.41.

on Mount Zempoaltepec in 1894. In 1934, Hellmayr placed Du Bus' Oaxacan records under *A. u. "unicolor"* (= *concolor*), but this action was certainly no more than surmise, for he examined no specimens.

TABLE 58
MEASUREMENTS OF *A. u. UNICOLOR*

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	16	161-172	166.0 \pm 0.8	3.1	1.8
		First-year..	3	157-162	159.3		
	F	Adult.....	14	154-165	158.6 \pm 0.9	3.5	2.2
		First-year..	4	152-159	154.7		
Tail	M	Adult.....	16	147-163	154.0 \pm 1.2	4.8	3.1
		First-year..	3	144-152	148.7		
	F	Adult.....	13	144-155	148.5 \pm 0.9	3.3	2.2
		First-year..	4	138-144	141.5		
Bill length	M	Adult.....	17	17.9-20.9	19.56 \pm 0.19	0.78	3.97
	F	Adult.....	15	17.7-20.0	18.56 \pm 0.18	0.69	3.74
Bill depth	M	Adult.....	15	10.0-11.4	10.60 \pm 0.09	0.36	3.41
	F	Adult.....	14	9.5-10.7	10.08 \pm 0.09	0.35	3.51
Bill width	M	Adult.....	16	9.0-10.2	9.79 \pm 0.08	0.31	3.13
	F	Adult.....	15	9.0-10.4	9.58 \pm 0.10	0.38	3.94
Tarsus	M	Adult.....	17	40.6-45.2	42.48 \pm 0.30	1.23	2.90
		First-year..	3	42.6-43.3	42.80		
	F	Adult.....	15	40.4-43.6	41.66 \pm 0.21	0.80	1.91
		First-year..	4	41.5-43.6	42.38		
Hind toe	M	Adult.....	17	14.1-15.9	15.22 \pm 0.12	0.49	3.21
		First-year..	3	14.8-15.1	15.00		
	F	Adult.....	15	13.8-16.0	14.86 \pm 0.17	0.67	4.49
		First-year..	4	14.5-15.6	15.12		
Middle toe	M	Adult.....	17	19.0-22.0	20.38 \pm 0.20	0.82	4.13
		First-year..	3	20.3-21.1	20.60		
	F	Adult.....	15	18.6-21.2	20.00 \pm 0.18	0.70	3.51
		First-year..	4	20.1-21.7	20.58		
Weights (gm.)	M	15	119-153	129.9		
	F	11	113-136	126.4		

On and near Mount Zempoaltepec, *A. u. oaxacae* occurs on the Caribbean slopes which support extensive forests of mixed hardwoods and pines above the main zone of subtropical cloud forest and along the upper altitudinal border of the latter formation. These two major formations do not occur juxtaposed elsewhere in Oaxaca. Occurrence of *A. unicolor* on the Sierra Madre del Sur farther to the west and on the highlands northward connecting central Oaxaca with the Sierra

Madre Oriental is therefore doubtful, since mountains of 10,000 feet elevation occur only in central Guerrero, where the race *guerrensis* is found, and in the southern part of the Sierra Madre Oriental, where the race *concolor* is found. *A. unicolor* is known to occur at elevations between 5,000 and 4,000 feet, but its presence at these lower elevations is not a basis, necessarily, for postulating dispersal or distributional continuity between races; in all known areas of occurrence the species lives on high mountain ranges or peaks or on Caribbean slopes of southern Mexican and Central American mountains.

Comparisons.—Compared with all available adult specimens of *concolor*, the two adults of *oaxacae* are darker than any *concolor* of either sex. One juvenal specimen of *oaxacae* differs distinctly from one of *concolor* (BS 144672); in color of both body plumage and flight feathers the juvenile of *concolor* falls between *unicolor* and *oaxacae*, but is closer to *unicolor*. Bill color of *concolor* does not differ from that of *unicolor*, and thus contrasts with that of *oaxacae*. In length of wing the three specimens of *oaxacae* are smaller than any available specimens of *concolor* of corresponding sex and age groups; but the sample of the latter race is so small that one can conclude only that the wing of *oaxacae* is not larger, and may even be smaller, than that of *concolor*. The two races do not differ in tail length; as a result, the wing-tail ratio of *concolor* is greater than 1 in all available adult specimens, and that of the two specimens of *oaxacae* is less than 1.

A. u. oaxacae is more similar to *guerrensis* than to any other race of *A. unicolor*. In color the adults of the two races differ only in that *guerrensis* is closer to Azurite Blue—Indulin Blue than to Cyanine Blue—Dusky Blue; juveniles differ only in that the flight feathers of *guerrensis* are only slightly more purplish. In length of wing and tail, all three specimens of *oaxacae* fall below all specimens of a good sample of *guerrensis* (table 60.) Thus, comparing the wing lengths of the three specimens of *oaxacae* with the averages of *guerrensis* of corresponding sex and age groups, the differences are 11.1, 11.1, and 4.8 mm., respectively; comparing the same dimensions of *oaxacae* with the smallest extremes of *guerrensis* of corresponding sex and age groups, the differences are 7, 7, and 1 mm., respectively. The tail of *oaxacae* is comparably shorter than that of *guerrensis* in the two adults of *oaxacae*, but proportionally more so in the single juvenal specimens. Bill and feet do not appear to differ in size.

Thus the characters of *oaxacae* are a combination of the color and the wing-tail ratio of *guerrensis* with a small wing, which is comparable in size with, or smaller than, that of *concolor* or *unicolor*. The expression of these characters is such that the few specimens available cannot be regarded as intergrades or even assigned to one of the presently recognized races, pending the acquisition of more material. Certainly I would not follow Hellmayr (1934:58) and place them together with "*unicolor*" (= *concolor*).

Aphelocoma unicolor concolor

Racial characters.—Compared with *unicolor*, slightly more purplish and approximately intermediate between *unicolor* and *oaxacae*. In size, similar to *unicolor* except in dimensions of feet, which are smaller (—5.1 per cent in adult males) and probably significantly so; wing longer than tail (ratio, 1.034:1); for dimensions see table 59.

Juvenal plumage: compared with *unicolor*, slightly darker; body plumage Chaotura Drab; flight feathers slightly more purplish, but still closest to Indigo Blue; only one specimen (BS 144672, female, Jico, Veracruz, July 6, 1893) available. Measurements (mm.) are as follows: wing, 157; tail, 152; tarsus, 39.6.

TABLE 59
MEASUREMENTS OF ADULT MALES OF *A. u. CONCOLOR*

	No. of specimens	Range	Mean
Wing.....	6	161-167	163.5
Tail.....	6	152-163	158.2
Bill length.....	6	18.1-20.2	19.35
Bill depth.....	6	9.7-10.8	10.35
Bill width.....	6	10.0-11.2	10.70
Tarsus.....	7	39.3-41.8	40.31
Hind toe.....	7	14.3-16.5	14.89
Middle toe.....	6	19.3-20.2	19.77

Geographic distribution.—Mountains of southeastern Mexico, in west central Veracruz, eastern México, and Puebla.*

Comparisons.—For a comparison of *concolor* with *oaxacae* see page 351.

Aphelocoma unicolor guerrenderis

Racial characters.—Compared with *unicolor*, darker and more purplish; body plumage Azurite Blue—Indulin Blue, tending toward Cyanine Blue—Dusky Blue. Larger in dimensions of tail (+11.0 per cent) and bill (+11.3 per cent in length); tail longer, not shorter, than wings (ratio, 0.975:1). (For dimensions see table 60.)

Juvenal plumage: compared with *unicolor*, darker and more purplish; body plumage Fuscous; flight feathers Nigrosin Blue. Tail longer, not shorter, than wings.

Geographic distribution.—Confined to mountains near Omilteme, Guerrero, in southwestern Mexico, at elevations of 7,000 feet or higher.

Comparisons.—For a comparison of *guerrenderis* with *oaxacae* see page 351.

Aphelocoma unicolor griscomi

Racial characters.—In color, intermediate between *concolor* and *guerrenderis*, thus darker and more purplish (Cyanine Blue—Dusky Blue) than true *unicolor*; chin less blue than in *unicolor* or any other race, gray streaking slightly lighter and extending over throat. Bill larger (+9.8 per cent in length in adult males) than in *unicolor*; wing longer than tail (ratio, 1.058:1). (For dimensions see table 61.)

No juvenal specimens of *griscomi* have been seen.

Geographic distribution.—Cordillera of northern El Salvador and Honduras, from Los Esesmiles and Mount Pucea east to Alto Cantoral and Rancho Quemado (see fig. 15); recorded at elevations of 8,000–8,500 feet in El Salvador and at 6,600 feet in Honduras. Judging by elevations given by Goodwin (1942:108) for

* Although I have examined no specimens of *A. u. concolor* collected more recently than 1893, it was collected in 1948 near Tezuitlán, forty miles northwest of Jalapa, Veracruz, by M. A. Traylor, Jr. (letter). Other recently taken specimens of this race may be contained in the Moore Collection.

TABLE 60
MEASUREMENTS OF *A. U. GUERRERENSIS*

	Sex	Age group	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	Adult.....	37	163-170	167.1 \pm 0.4	2.1	1.3
		First-year..	8	157-165	161.1		
	F	Adult.....	28	161-168	164.8 \pm 0.4	1.9	1.1
		First-year..	9	155-165	159.7		
Tail	M	Adult.....	37	164-179	171.3 \pm 0.6	3.6	2.1
		First-year..	7	160-170	166.0		
	F	Adult.....	28	161-175	165.9 \pm 0.6	3.0	1.8
		First-year..	8	157-165	163.4		
Bill length	M	Adult.....	38	20.1-23.4	21.72 \pm 0.14	0.87	4.01
		First-year..	7	19.5-22.1	21.38		
	F	Adult.....	28	19.7-22.6	20.91 \pm 0.14	0.73	3.50
		First-year..	7	19.4-22.9	20.84		
Bill depth	M	Adult.....	37	10.4-12.2	11.47 \pm 0.06	0.37	3.20
		First-year..	7	10.8-11.5	11.24		
	F	Adult.....	28	10.3-11.7	11.06 \pm 0.06	0.31	2.80
		First-year..	7	10.7-11.5	11.17		
Bill width	M	Adult.....	38	9.8-11.6	10.73 \pm 0.07	0.41	3.80
		First-year..	7	9.7-11.1	10.48		
	F	Adult.....	28	9.8-11.7	10.68 \pm 0.08	0.43	4.03
		First-year..	7	9.7-11.0	10.30		
Tarsus	M	Adult.....	38	39.3-43.0	41.57 \pm 0.16	1.01	2.43
		First-year..	8	38.1-42.0	40.90		
	F	Adult.....	28	39.2-41.8	40.68 \pm 0.12	0.63	1.54
		First-year..	9	37.0-42.0	40.30		
Hind toe	M	Adult.....	38	13.8-15.5	14.75 \pm 0.05	0.34	2.28
		First-year..	8	14.2-15.2	14.52		
	F	Adult.....	28	14.1-15.2	14.62 \pm 0.06	0.34	2.32
		First-year..	9	14.1-14.8	14.54		
Middle toe	M	Adult.....	38	19.3-21.0	20.19 \pm 0.08	0.47	2.32
		First-year..	8	19.1-20.6	19.97		
	F	Adult.....	28	19.4-20.8	19.86 \pm 0.08	0.41	2.04
		First-year..	9	19.2-21.0	19.83		

collecting localities in Honduras of C. F. Underwood, who obtained all the specimens of *A. unicolor* available to me from that country, *A. unicolor* may range as low as 4,500 feet (Cerro Santa María, *ibid.*: 109).

Comparisons.—All available adult males of *griscomi* are slightly less purplish than the one male of *oaxacae*; females of *griscomi* are similar to the one of *oaxacae*. Thus in color *griscomi* is probably similar to or slightly less purplish than *oaxacae*; in size *griscomi* is larger than *oaxacae*, at least in dimensions of wing and tarsus.

Geographic variation and intergradation.—The five presently recognized races of *A. unicolor* are distinct entities between which no intergradation is known. As noted by Dickey and van Rossem (1938:409), the Isthmus of Tehuantepec separates them into two groups: first, *unicolor* and *griscomi*; second, *concolor*, *oaxacae*, and *guerrerensis*. Intergradation is improbable (between *concolor* and *oaxacae*, *unicolor* and *griscomi*) or definitely nonexistent (between *guerrerensis* and *oaxacae*, *oaxacae* and *unicolor*).

TABLE 61
MEASUREMENTS OF ADULTS OF *A. U. GRISCOMI*

	Sex	No. of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	M	27	160 -174	167.9 \pm 0.6	3.2	1.9
	F	21	156 -167	161.5 \pm 0.6	2.9	1.8
Tail	M	27	150 -166	158.7 \pm 0.7	3.8	2.4
	F	21	148 -160	153.7 \pm 0.7	3.2	2.1
Bill length	M	26	20.2- 23.3	21.48 \pm 0.15	0.74	3.46
	F	19	20.0- 22.7	21.16 \pm 0.17	0.76	3.59
Bill depth	M	27	10.4- 11.8	11.01 \pm 0.08	0.41	3.71
	F	17	10.3- 11.5	10.90 \pm 0.08	0.33	2.99
Bill width	M	27	10.2- 11.7	10.76 \pm 0.08	0.41	3.80
	F	19	9.8- 11.6	10.70 \pm 0.11	0.47	4.41
Tarsus	M	27	40.0- 44.7	42.53 \pm 0.27	1.41	3.32
	F	21	40.1- 44.1	42.02 \pm 0.24	1.10	2.62
Hind toe	M	27	14.2- 16.0	14.90 \pm 0.09	0.47	3.14
	F	21	14.1- 15.4	14.82 \pm 0.10	0.45	3.05
Middle toe	M	26	19.5- 21.9	20.91 \pm 0.12	0.64	3.04
	F	21	19.0- 21.1	20.09 \pm 0.13	0.58	2.86

In differences of color the five races present a seemingly anomalous situation in that the geographic extremes, the purplish races *guerrerensis* and *griscomi*, are separated by intervening less purplish (*concolor*) or more bluish (*unicolor*) races (Dickey and van Rossem, 1938:408). Further, the race *oaxacae*, which is as purplish as *griscomi* or slightly more so, geographically separates *unicolor* from *concolor*. These facts suggest strongly that the ancestral form of *unicolor* was more similar to the three purplish races than to *concolor* or *unicolor*. The distribution of the ancestral form was probably continuous at one time. The races *concolor* and *unicolor* would thus represent independent color differentiates, *unicolor* having diverged from the ancestral form farther than *concolor*.

In characters of size there is little evidence of geographic trends. All five races are large, and differences in proportions for the most part are slight. A striking departure of *guerrerensis* from the other four races is in increased size of tail,

which appreciably exceeds the wings in length. (See fig. 16.) Among the other races, length of tail does not appear to vary significantly. *A. u. unicolor* has the shortest tail, but not the shortest wing, of all five races; it thus has the highest wing-tail ratio (1.072:1).

Length of wing does not differ significantly among the races *griscomi*, *unicolor*, and *guerrerensis*. The data in figure 16 suggest that in *concolor* the wing is significantly shorter; this is not unlikely, since in the neighboring race, *oaxacae*, wing lengths of available specimens fall below those of *concolor*.

In bill length, *concolor* and *unicolor* (and probably *oaxacae*) have smaller bills than the geographic extremes. (See fig. 16.) In tarsal length, however, the five

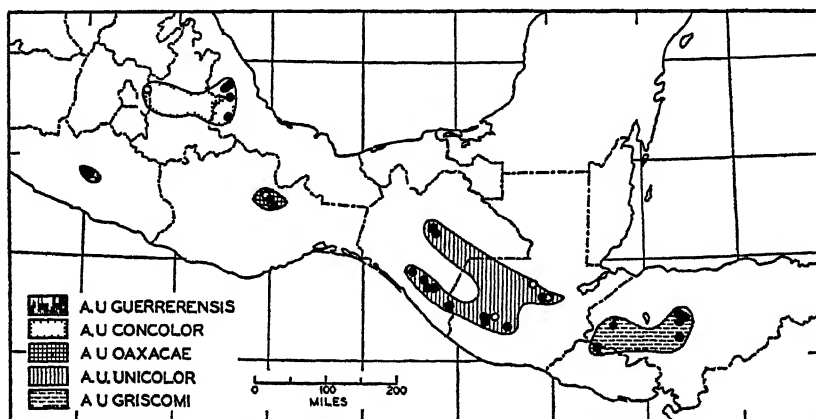


Fig. 15. Distribution of races of *Aphelocoma unicolor* in southern Mexico and Central America. Dots indicate localities represented by specimens; circles, localities reported in the literature; squares, type localities.

races are divided into two groups by the Isthmus of Tehuantepec, those to the northwest having shorter tarsi than those to the southeast.

There is thus little consistency in the variation observed among characters of the five races. Two distinct color differentiates are interposed between three closely similar purplish races; moreover, in size the geographic extremes are larger in most dimensions than the intervening forms. It seems possible that the ancestral, more widely distributed population of *A. unicolor* underwent restriction and subdivision throughout its extent at approximately the same geologic time, and that the five presently known races became differentiated from the parent form to varying degree over approximately the same period of time. When seriated geographically, the sequence from northwest to southeast is *guerrerensis*, *concolor*, *oaxacae*, *unicolor*, and *griscomi*; in this sequence the five races are relatively well marked, suggesting insular differentiates rather than those of continental, ecologically contiguous areas. When seriated according to color, the sequence from most to least purplish is *guerrerensis*, *oaxacae*, *griscomi*, *concolor*, and *unicolor*. When seriated according to size, the sequence from largest to smallest is *griscomi*, *guerrerensis*, *unicolor*, *concolor*, and *oaxacae*; the last may prove not to differ significantly in size from *concolor* when adequate series of specimens are available.

No instances of significant intraracial variation are evident in the material available to me. Only the races *unicolor* and *griscomi* could be tested in this respect; although data for each of these races were at first divided according to geographic subgroups and analyzed separately, observed differences were either insignificant or barely significant for one sex only—a result attributable at present more to the statistical inadequacy of the available material than to any possible intraracial variation. For these reasons, data within the races *unicolor* and *griscomi*, respectively, were combined. Available maps of Central America strongly suggest that the highland areas inhabited by *unicolor* and *griscomi*, respectively, are more or less continuous, and that population interchange within each race is not impeded to the extent that significant intraracial differences occur; but of course these are

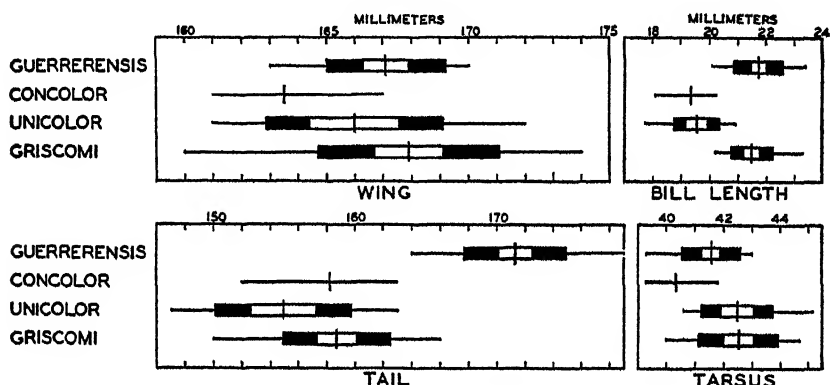


Fig. 16. Individual and geographic variation in races of *Aphelocoma unicolor*. Data arranged from northwest to southeast, and based on adult males.

suppositions that need tests based on adequate series of specimens. The available data suggest further the possibility that both races occur at lower elevations than the more northwestern races; if this proves to be true, there is added reason for absence of significant intraracial variation.

Characters suggestive of plumage pattern in A. coerulescens and A. ultramarina.—Five juvenal specimens of *guerrerensis*, one of *oaxacae*, and one of *concolor*, all in the earliest stage of postjuvenal molt and younger than any other juveniles available to me, show a faint, broad band across the upper chest. All under parts are dull blackish brown. The pectoral band is formed by a slight overcast of purple. The existence of this indistinct, broad band is noteworthy, since in the Mexican jay (*A. ultramarina*) and in the juvenal plumage of the southern Mexican races of the scrub jay (*A. coerulescens*) a comparably broad and indistinct, but darker band is evident.

In the adult plumage of *A. unicolor* the back is duller than the head, and suggests the contrast between back and head in both *A. coerulescens* and *A. ultramarina*. The degree of contrast is slight in *unicolor*; in this respect it is more similar to *ultramarina*.

The gray streaking of the throat in *unicolor* is essentially similar to that seen in *coerulescens* in that in both species the feather vanes are dark laterally, light

medially. This contrast is absent or obsolescent in *ultramarina*. In all three species the shafts of the throat feathers are black.

Blue coloration of *unicolor* is considerably more intense and more purplish than that of any Mexican race of either *coerulescens* or *ultramarina*. (See frontispiece.) Only the less purplish, lighter *A. u. unicolor* approaches a dark extreme in one of the other species, *A. u. ultramarina*. Although the shade of blue is approximately the same, it differs between *unicolor* and *ultramarina* in intensity. However, this similarity does not indicate, in my opinion, special affinity, for I regard *unicolor* to be a color differentiate derived from a purplish form ancestral to all the races of this species.

Ecologic distribution.—Throughout most of its range, *A. unicolor* is apparently local in distribution and occurs in cloud forests of high mountains or, at lower altitudes, in similar vegetation on Caribbean slopes of large mountain masses. *A. unicolor* is apparently a permanent resident, remaining associated with the cloud forest at all times of the year. The areas of lower altitude and unsuitable habitat which separate the five races from each other probably act as complete interracial geographic barriers. In Oaxaca and Guerrero, *unicolor* may overlap altitudinally with *coerulescens*. In México, Puebla, and Veracruz it evidently overlapped in vertical distribution with *ultramarina* and possibly also with *coerulescens*.

In central Guerrero, *unicolor* inhabits the humid hardwood forest at high elevations on the Sierra Madre del Sur (Nelson, 1903:154);³⁰ in Chiapas, the humid forests of mixed pine and broad-leaved trees (P. Brodkorb, letter); in Guatemala, cypress and pine forests (Griscom, 1932:403; Wetmore, 1941:526, 557); and in El Salvador, the dense montane forests of gigantic pines, evergreen oaks, and other hardwoods (Dickey and van Rossem, 1938:51, 409). The habitat of *A. unicolor* differs from that of the other two species in that it is a humid, tall, luxuriant forest rather than a relatively dry, open woodland or chaparral. But, like the other two species of *Aphelocoma*, *A. unicolor*, although it is associated primarily with one major vegetational type, frequents bordering habitats of contrasting kind in the course of its normal activities. Observations recorded by J. T. Marshall, Jr., on Los Esesmites, El Salvador, in March, 1942, indicate that small flocks of six to eight individuals may occur in open areas of shrubs and scattered pines as well as in dense forests. It appears, thus, that here the cloud forest serves as the essential headquarters of the species and that adjacent, more open habitats may be frequented to varying degree. But to what extent this is true in races the distribution of which overlaps or adjoins that of *A. coerulescens* (as in *A. u. oaxacae* and *A. u.*

³⁰ Near Omilteme, Guerrero, in the period from April 27 to May 2, 1950, *A. u. guerrensis* was not located, although the available habitats seemed adequate for it, at least locally, in the light of observations in Chiapas. The racial characters peculiar to the Guerrenan population (darkest, most purplish coloration; large size; longest wing and tail; highest wing-tail ratio) suggests that here *unicolor* is probably a species of the dark, undisturbed temperate cloud forest of enormous hardwoods and pines. From our experience and the suggestive evidence just given, I am led to assume that the ecological range of *guerrensis* is narrower than that of the nominate race. All the areas accessible to us where formerly virgin upland pine-oak forest occurred are now opened and even cleared locally through selective cutting of sugar pines. Understory vegetation is reduced to scattered small trees and islands of brush in which *Pipilo ocai* and *Atlapetes pileatus* are common. W. W. Brown, the veteran collector living at Chilpancingo, Guerrero, agrees that this may explain the scarcity, if not absence, of *guerrensis* at Omilteme, and adds, in a recent letter, that another important factor is persistent shooting of larger birds by lumbermen for food.

guerrercensis) is not known at present. In one race (*A. u. concolor*), overlap with both of the other species of *Aphelocoma* occurred, if it does not now, and competition with a race of the Mexican jay (*A. u. ultramarina*) of comparable size also inhabiting high montane forests, combined with gradual restriction of those forests by man, may well have been critical factors in local range contraction."

DISCUSSION OF VARIATION

INTERRACIAL CORRELATION OF DIFFERENTIATION

In his study of the genus *Junco*, Miller (1941:357) found interracial differences between lengths of wing and tail closely correlated (fig. 17). Such correlation occurred throughout the genus, irrespective of degree of differentiation in other characters. Evidence from the genus *Aphelocoma* differs significantly. Thus, interracial correlation among races of *A. coerulescens* is evident in the "*californica*" group and in the northern forms of the "*woodhousei*" group; but a striking departure is evident in the Floridan race *coerulescens*, in which wing length is shorter than in any other form of *Aphelocoma*, but tail length remains the same as that of Texan, Rocky Mountain, and Great Basin races. A second departure from a consistent interracial correlation is evident among the Mexican races of *A. coerulescens*, in which there is a definite trend toward increase in wing length proportionally greater than that in tail length. The extreme of this trend, *remota*, of Guerrero, thus displays the highest wing-tail ratio among races of *A. coerulescens*, a character suggestive of *A. ultramarina*, in which the wing-tail ratio is higher. It may be noted further that *remota* stands closer to *ultramarina* in wing-tail ratio than it does to the small-winged race, *coerulescens*, here placed in the same species as *remota*. In *A. ultramarina*, interracial correlation of wing and tail is consistent. This is apparently true also in *A. unicolor*, except in the race *guerrercensis*, in which the tail is proportionally longer. Wing-tail proportions may be judged in figure 17 by marking off a line between wing and tail averages in the *californica* column;

¹¹ Certain points from observations on *A. u. unicolor* in central and southern Chiapas, March 27-April 20, 1950, should be mentioned here, however briefly. My records on habitat distribution in the main support the text account based on the literature for the species as a whole. In southern Chiapas (28 mi. ESE Comitán), *unicolor* occurs fairly commonly and as low altitudinally as 4,900 feet. It is present in all types of pine-oak forest, even relatively open, woodland-like stands, both modified and natural. It is absent from sparse and grove-like stands of pines and oaks on dry sites, usually steep southwest exposures, and from flat, grassy woodlands of pure pine. In the latter habitat *Cyanocitta stelleri* is present. In an area six miles southeast of San Cristóbal, the optimal habitat appears to be the relatively undisturbed forests of large pines, oaks, and madrones such as are now confined to steep and high slopes, here reaching at least 7,500 feet. The upper strata of the forest are not dense, as the trees are more or less open below the broken canopy, but the understory vegetation is well developed. Groves of trees on flat areas with understory of no more than herbs and scattered shrubs are generally avoided, and again, in such situations *Cyanocitta* occurs. *A. unicolor* feeds at all levels in trees below the uppermost part of the canopy and also on the ground. Foraging in dense epiphytic growth along large oak limbs, especially among bromeliads, was observed frequently.

Virtually nothing is on record in the literature concerning the behavior of *A. unicolor*. I found it to be similar to that of *A. ultramarina*. The common call note of the latter, a distinctive finch-like "rink," which I have heard from *A. u. arizonae* (Arizona and Sonora), *wollweberi* (Durango), and *sordida* (Hidalgo), is also the usual note of *A. unicolor*. Spaced groups of up to nine unicolor jays, including adults and first-year birds, were found settled in more or less restricted areas where they could be relocated, as in *ultramarina*. In the area of each of two such groups, a nest with eggs was found; in a third area, a group of jays was attending at least two fledglings. In all details in these observations and others, *unicolor* resembles *ultramarina*. The phylogenetic relationship of the two would appear to be even closer than the morphological evidence alone indicates.

when the distance between averages is less than the length of this line, the wing is longer than the tail, and vice versa.

Interracial correlation in foot dimensions is consistent throughout the genus except in two races of *A. coerulescens*. In *cactophila* of central Baja California the

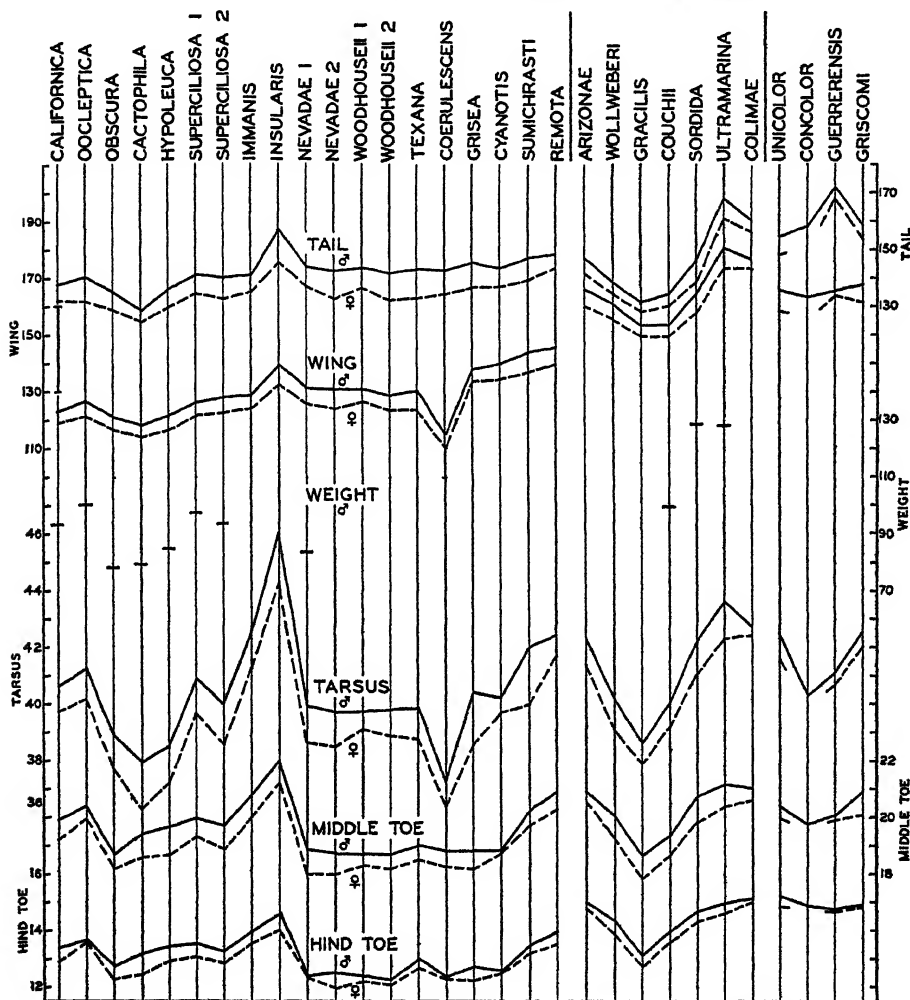


Fig. 17. Comparison of average lengths (mm.) of tail, wing, tarsus, middle toe, and hind toe in races and species of genus *Aphelocoma*. Average weights (gm.) indicated by transverse line for certain races only. Key to intraracial subdivisions: *superciliosa* 1, San Joaquin Valley and adjoining foothills; *superciliosa* 2, northeastern California, bordering parts of Nevada, and south-central Oregon; *nevadae* 1, Nevada and western Utah; *nevadae* 2, Arizona; *woodhousei* 1, Colorado, eastern Utah, and northern New Mexico; *woodhousei* 2, southern New Mexico, western Texas.

tarsus is shorter than in other races of the "*californica*" group, but lengths of hind and middle toes are shorter in *obscura*, the race to the north. In *coerulescens* of Florida the tarsus is short, whereas hind and middle toes do not differ from those of races to the west. Slight correlation occurs between tarsus and wing. That be-

tween tarsus and tail is even smaller, there being one instance of negative correlation in *griscomi*. Correspondence between tarsus and weight is fairly close; of the dimensions used commonly in avian systematics, tarsal length is the best index to relative body mass, but the correlation may not prove to be consistent when adequate weight data are available. This is suggested by absence of correlation between tarsus and weight in *cactophila*. Moreover, correlation may vary in degree between populations of the same race which do not differ in dimensions; thus, in *nevadae* of the Great Basin, averages based on specimens from southern Nevada are 4.5 and 3.9 gm. less in males and females, respectively, than those based on northern specimens (table 30).

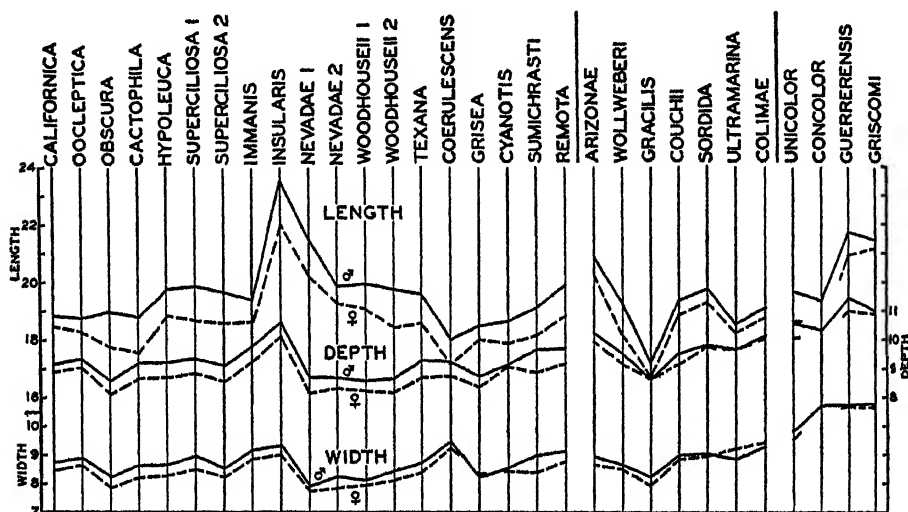


Fig. 18. Comparison of average measurements (mm.) of length, depth, and width of bill in races and species of genus *Aphelocoma*.

In dimensions of the bill (fig. 18), close correspondence between width and depth is evident throughout the genus, except in *coerulescens*, in which the bill has become strikingly broad; in depth of bill, however, *coerulescens* is similar to *texana* and races of the California mainland. In *A. unicolor concolor*, depth is relatively small in relation to width when this race is compared with others of the same species. The sample of *concolor* is small, and reduction in depth seems worth noting only because a corresponding reduction in length suggests that the proportions of the bill may prove to differ significantly from those of other races.

A varying degree of correlation is displayed between bill length and other bill dimensions. In *superciliosa* and *hypoleuca*, increase in bill length is not accompanied by correlated change in depth and width. Increase in length of bill in *insularis* is correlated with increase in depth of relatively smaller magnitude, whereas increase in width is slight. Negative correlation of length and depth is evident in *nevadae*, *woodhouseii*, and *texana*; among these races there is a tendency for the bill to become long and basally small. In *coerulescens* a striking negative correlation occurs between length and width; this race has the shortest and widest bill of all

racess of *A. coerulescens*. Among races of *A. ultramarina*, correlation between bill dimensions is consistent, except in *gracilis*, in which the bill is relatively shorter than in other races. A seeming discrepancy in a comparison of *ultramarina* and *colimae* with the remaining, long-billed forms of *ultramarina* is explained in part

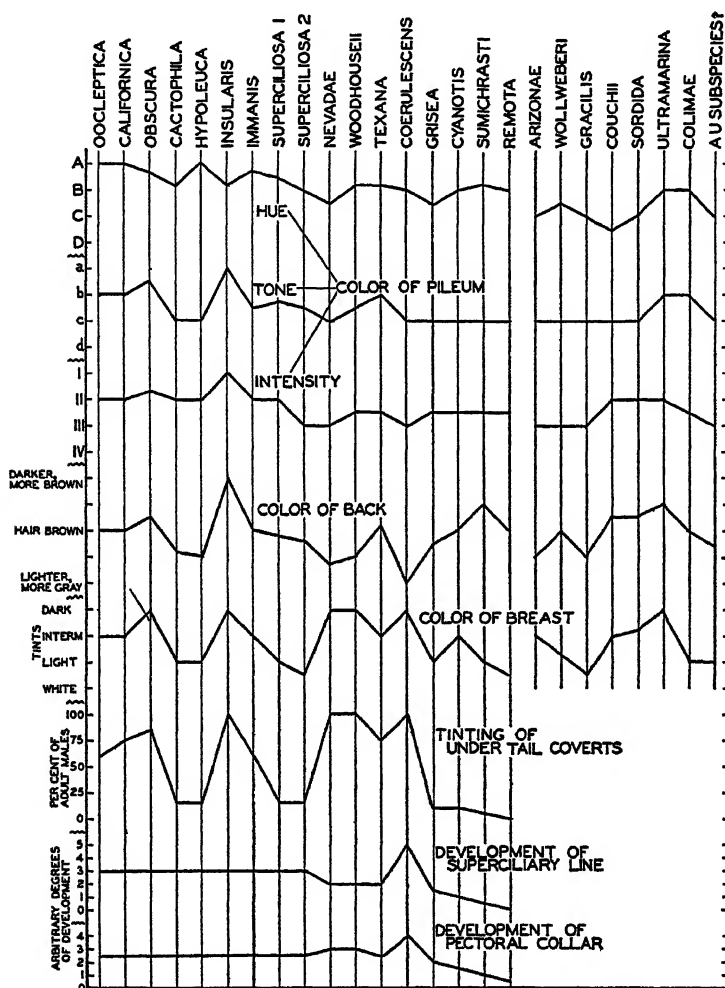


Fig. 19. Graphic comparison of average color characters of races of *Aphelocoma coerulescens* and *A. ultramarina*. Units for upper three lines showing interracial differences in hue, tone, and intensity of blue color of pileum are based on Ridgway's standard colors and color scales. (See text, p. 201.)

by the position of the nostril. (See p. 342.) In *A. unicolor*, differentiation in length of bill of *guerrerensis* has progressed farther than in depth, whereas width is similar to that of other races.

Interracial correlation of color and pattern characters is illustrated in part in figure 19. Within the "*californica*" group of races a variable correspondence is observed between hue, tone, and intensity of the blue color of the pileum. Negative

correlation between hue, on the one hand, and tone and intensity, on the other, is observed in the dark races *obscura* and *insularis*. It would appear that the most heavily pigmented races are not actually the most purplish, a point which needs to be investigated through comparative study of pigment distribution. Positive correlation between shade and intensity indicates that the darkest races tend to be the least gray, and vice versa.

Among remaining races of *A. coerulescens* there is less interracial differentiation in color of pileum than among races of the "*californica*" group. Negative correlation between hue and intensity in *grisea* indicates that the bluest forms are not necessarily the grayest, a fact which is more strikingly shown by *couchii* among races of *A. ultramarina*. Otherwise, correlation among hue, tone, and intensity of blue, in *A. ultramarina* as well as *A. coerulescens*, is positive or it is zero. These interracial comparisons reveal that differentiation in color may occur in only one of the basic scales or in any combination of them. (See frontispiece.)

Color of back correlates most closely with tone of blue. Correlation is positive or zero. Variation in color of the back is based on several tones of grayish brown, the darker tones being reached by addition of black and loss of neutral gray. Slight positive correlation is evident between hue of pileum and color of back in the Mexican races of *A. coerulescens* and in most of the races of *A. ultramarina*.

Interracial differences in color of breast (see fig. 19) refer to tints of the brownish-gray wash over the breast below the pectoral collar. Within the "*californica*" group, color of breast correlates with color of back and tone of blue. In the remaining races of *A. coerulescens*, however, color of back is more or less independent of color of breast. In *A. ultramarina* the degree of correlation is variable; negative correlation occurs only in the "*wollweberi*" group.

Interracial differences in characters of the under tail coverts are of two kinds: first, differences in color; second, differences in frequency of tinting. In the first character, racial differences correspond to those in color of pileum, as do all other blue or bluish areas; but in the second character they correspond to differences in color of breast.

Differences in development of the superciliary line and pectoral collar are primarily evident among racial groups. Compared with the superciliary line of the "*californica*" group, that of interior and Mexican races is reduced. Gradual reduction reaches an extreme in *remota*. In *coerulescens* of Florida the superciliary line is broad and prominent; in this instance the extreme degree of its development is apparently related to the whitening of the forehead, the light-colored forehead and superciliary lines being continuous.

Development of the pectoral collar is correlated with that of the superciliary line throughout *A. coerulescens*, except in *woodhouseii* and *nevadae*, in which the pectoral collar may be said to be developed to a greater degree than in members of the "*californica*" group in that the total quantity of blue in the mid-region of the collar is greater.

In *A. unicolor*, interracial differences in color are primarily those of hue. But one other significant interracial difference in color or pattern occurs, that in streaking of the throat, which is most extensive in *grisei*. This character does not appear to correlate with color of body plumage.

In summary, interracial correlation among several characters of color and pattern occurs within geographic groups of races, but the independence of modification of these characters is evident in intergroup correlation.

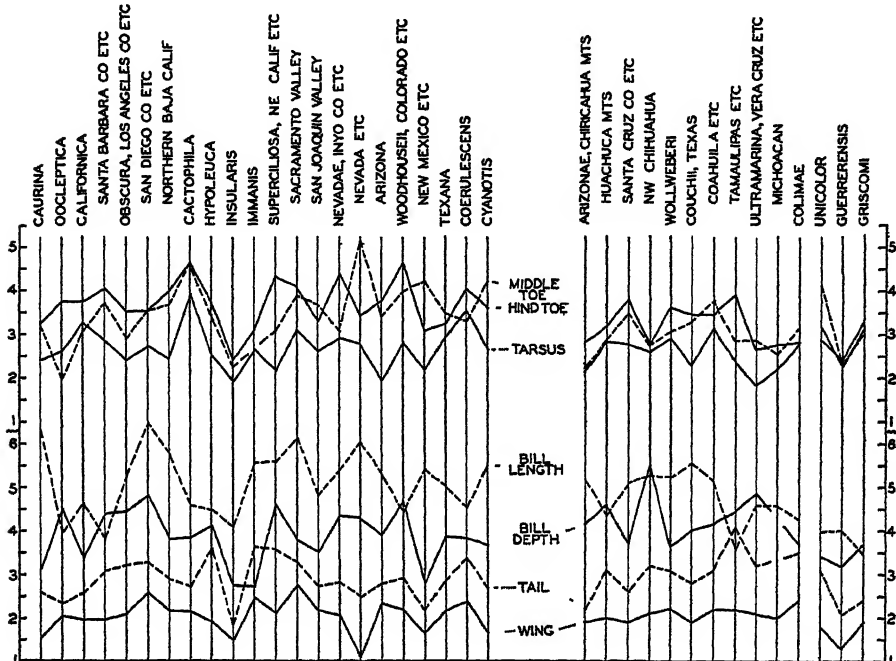


Fig. 20. Comparison of coefficients of variability of mensural characters of adult males among races of *Aphelocoma coerulescens*, *A. ultramarina*, and *A. unicolor*.

INTRARACIAL VARIABILITY

Variability of mensural characters in *Aphelocoma* agrees remarkably with that demonstrated by Miller (1941:365) in *Junco*. The wing varies least. Variability of tail, bill depth, and bill length is successively greater. The results shown in figure 20 indicate that in *Aphelocoma*, unlike *Junco*, bill length is more variable than bill depth. Wing and tail vary less than in *Junco*. Variability of the tarsus is generally more comparable to that of the tail than, as in *Junco*, to that of the wing. Middle toe and hind toe are successively more variable than the tarsus, as in *Junco*; variability of tarsus is approximately comparable in *Aphelocoma* and *Junco*, but that of middle toe and hind toe is less in *Aphelocoma*. Irregularities in variability of bill depth and bill length and of middle toe and hind toe occur somewhat more frequently in *Aphelocoma* than in *Junco*.

Of the populations of different races and species the variability of which is shown in figure 20, the most restricted are *A. c. insularis* and *A. u. guerrierensis*. The first and probably the second consist of small unit populations each of which is expected to be comparatively homogeneous in genetic make-up. Reduced varia-

bility in wing, tail, and foot dimensions indicates such homogeneity. Variability in bill dimensions, however, does not differ from that of other races.

Degree of variability in color, although not subjected to statistical study and analysis, can be said to display interspecific and interracial differences. In general, color in *A. ultramarina* and *A. unicolor* varies to a comparable degree, but in *A. coerulescens* variability is greater, at least in the North American races of which abundant material was examined. Races of the "*californica*" group display the greatest intrapopulation variability; this is particularly true of *A. c. superciliosa*. In part, at least, this variability is to be explained by the diversity of climate and habitat over the large area occupied by these races and also by the relative ease of genetic interchange due to relative continuity of distribution.

Color characters are relatively stable throughout the genus. No distinctive variants suggesting conspicuous mutations have been detected. Instances of partial albinism are exceedingly rare. Among races of the "*californica*" group, particularly in *cactophila* and *hypoleuca* (see p. 242), foreheads of occasional specimens are whitened to varying degrees. In the Floridan race *coerulescens*, whiteness of forehead is a conspicuous character. Appearance of this character in occasional scattered individuals of the Pacific coast races would suggest that it is a latent recessive character, complexly controlled, as are most quantitative characters, the genetic basis of which is of wide distribution among the Pacific coast races.

SEXUAL DIMORPHISM

No absolute differences between sexes occur in *Aphelocoma*. Females are smaller (figs. 17-18) and duller, but the degree of difference varies among races and species. Irregularities in the direction of difference among Mexican races are due, in my opinion, to the inadequacy of material available to me. In all characters, the sexes in *A. ultramarina* and *A. unicolor* differ less than in *A. coerulescens*.

In *A. coerulescens*, average lengths of wing and tail differ in the sexes, in general, by 4 or 5 per cent. Among the interior races, average difference in length of tail tends to be greater (between 7 and 8 per cent) than among the coastal races. In *A. ultramarina* and *A. unicolor* the differences in both wing and tail generally amount to 2 or 3 per cent. Average lengths of tarsus, middle toe, and hind toe tend to differ by 2 or 3 per cent in *A. coerulescens*; by 1 or 2 per cent in *A. ultramarina* and *A. unicolor*. Average differences in bill dimensions vary interracially to a greater degree than do other measurements. In *A. coerulescens* these amount to 2 to 6 per cent. In *A. ultramarina* and *A. unicolor* the average difference in length never exceeds 3 per cent; those in depth and width are usually comparable, but occasionally reach 5 or 6 per cent.

Average differences between sexes in blue coloration appear to be primarily those of intensity and, at least among the darker races of *A. coerulescens* along the Pacific coast, also of hue. In races in which under tail coverts may be tinted or white, frequency of tinting is lower in females than in males. But one difference in pattern is known: in *A. coerulescens* the pectoral band of females is reduced in that the area of dark pigmentation is smaller and the pigmented parts are less blue and more brownish gray. In certain races, as in those of the "*californica*" group, this often results in an incomplete band in females, whereas in males the band is almost

always complete. Colors of back and of under parts exclusive of pectoral band and under tail coverts do not differ in the sexes. In *A. unicolor* and *A. ultramarina* the sexes differ in color only in average grades of blue or purplish blue. There are no differences in pattern between sexes in the two species.

ENVIRONMENTAL CORRELATION

Interracial differences in color provide partial support for Gloger's rule in that degree of pigmentation is associated, in general, with humidity and rainfall. Among races of *A. coerulescens* the darker, more brownish, and more purplish forms occur in more humid regions. Among races of the "*californica*" group the association is evident also in color tone of the breast and in the frequency of tinting of under tail coverts. Gloger's rule is also illustrated by variation in *A. ultramarina*.

Evidence for Allen's rule—the principle of relative increase in size of extremities from north to south—is not satisfactory because adequate data on body size are lacking for Mexican races. Available data on size of bill and feet in relation to body mass do not provide any confirmation of Allen's law in either *A. coerulescens* or *A. ultramarina*.

Although the principle of Allen's rule does not apply, at least not directly, to the wing and tail in birds, the general pattern of geographic variation in these structures with reference to body size may be summarized here. Races with shortest wings are found along the Pacific coast and in Florida; those with longer wings are interior or Mexican. Progressive increase in length of wing and tail in races of the "*woodhousei*" and "*sumichrasti*" groups is probably not accompanied by a corresponding increase in body size. Meager data (tables 36 and 37) suggest that in weight, *sumichrasti* and *remota* do not differ from the larger mainland races of the "*californica*" group. In *A. ultramarina*, wing and tail are relatively longer in the southern races than in the northern races, but again the available data on body size indicate that in this character the race *ultramarina* and the northernmost populations of *arizonae* are more or less comparable.

Bergmann's rule—the principle of relative decrease in body size from north to south—is confirmed by evidence from the genus *Aphelocoma* to a partial degree. Because of relative constancy of environmental conditions over the geographic range of each species that is indicated by the character of the vegetation, it is necessary to examine not the southernmost races, but rather those living in the warmest climates to determine whether Bergmann's principle is illustrated by members of this genus. The warmest regions of considerable extent are central Baja California and Florida. Within the "*californica*" group, the smaller races are coastal, not southern; but the smallest, *cactophila*, occurs in central Baja California. At low elevations in the Cape region of Baja California, temperature conditions are probably more or less comparable to those of the central part of the peninsula, but scrub jays are distributed from sea level to the highest parts of the Sierra de la Laguna, where the climate is cooler. Under these circumstances, operation of Bergmann's law is obscured by the relatively sharp change in climate over a given area throughout which a more or less freely interbreeding population of the scrub jay occurs. The same interpretation applies to other warm regions in-

habited by *A. coerulescens* where the resident race is not small in body size, as, for example, in the southern part of the San Joaquin Valley.

Body size of *coerulescens* of Florida is approximately the same as that of *cactophilus*. Temperature averages of Florida are more or less comparable to those of central Baja California (Nelson, 1921; Kincaid, 1928).

In *A. ultramarina* the smallest race, *gracilis*, occurs in the west-central part of the range of the species as a whole; larger races occur to the north, south, and east. Bergmann's principle cannot be tested by this example, however, since adequate data on regional temperature differences in Mexico are not available.

The degree to which detailed study of given species or groups of species provides data which support any of these ecological rules depends, in the main, on the climatic relations and distributional history of each species as a whole. I would not minimize their general significance by emphasis on the meager support afforded by *Aphelocoma*. Environmental correlations which are of more immediate significance in an interpretation of geographic differences are those which consider the characteristics of the habitat, physical and biotic, in relation to the habits and life requirements of the species (Miller, 1931:102, 1941:365; Engels, 1940:343). Among races of the "*californica*" group the differences in body size and in length of wing and tail appear to me to be related to the comparative density of the scrub and woodland vegetation which is characteristically inhabited by *A. coerulescens*. The smaller races are those of the coast, along which relatively tall and more or less compact chaparral is more extensive, wooded areas are more dense, and understory vegetation is better developed than in the interior of California. It would appear that small size and consequent ease of passage through dense vegetation may be favored by selection. The influence of this factor is probably strengthened by the restrictive effect of the vegetation on the degree of local dispersal and population interchange, with the result that interbreeding with the larger, longer-winged valley race is deterred. Thus the character of the vegetation is a factor tending partially to isolate coastal populations and so to conserve the results of selection which favors smaller birds. The consequence is reduction in size, particularly in length of wings and tail.

The inland races *superciliosa* and *immanis* are larger, and in populations east of the Sierra Nevada the wing is relatively longer. These differences, I would suggest, are in part at least linked with the more open character of the vegetation due to a less humid climate and to a greater interspersion of scrub and woodland with grassland. Under these circumstances the flights of scrub jays would tend to be more frequent and longer. This interpretation seems substantiated by the greater wing length of the races *nevadae* and *woodhousei* which live chiefly in the piñon woodland and chaparral on the lower slopes of the Great Basin ranges and the Rocky Mountains. In these races the factor of vegetational density influences wing size in the same direction as in *superciliosa*. Moreover, comparatively extensive post-breeding dispersal of first-year birds and possibly a certain amount of vertical or latitudinal migration occur in *nevadae* and *woodhousei*. (See pp. 282, 291.) Conceivably, this dispersal may be of long-range value to the survival of these interior races in that a portion of the population spends the winter at low elevations where winter climatic conditions are not so extreme as those at higher

elevations. Selection may thus favor individuals of these interior races which move comparatively long distances in the fall or winter to elevations below those of the breeding range. This added factor would also tend to favor increase in size of wing.

The Floridan race *coerulescens* is noteworthy in this regard. Extreme shortness of wing in this race suggests adjustment to a dense scrub of local distribution. The shortened tarsus appears to be a further adjustment to the low-lying, compact character of much of the scrub. The relatively long tail, however, is indicative of a compensatory adjustment among the wing, tail, and body which is different from that of western races. Body size, tarsus, and wing are proportionally smaller than in western races, but the tail is of comparable length. *A. c. coerulescens* suggests a nonmigratory thrasher (Mimidae) in these proportions. In *Toxostoma redivivum* (Engels, 1940:348), for example, the long tail appears to be of importance in movement through bushes and particularly in climbing through brush. Thus the Floridan scrub jay may spend more time within plant cover and on the ground than any of the other races; proportions of the extremities certainly suggest that it differs in locomotory habits.

Among the coastal races of the "*californica*" group, *oocleptica* of the San Francisco Bay region is the largest. Populations of this race average larger than those of the Sacramento Valley, although the range of variation of the latter in dimensions of wing and tail includes that of the former. Thus, *oocleptica* seems at first sight to be a puzzling exception to the foregoing situations in that it is a coastal race, presumably subject to the same environmental influences as *californica* and *obscura*, but it is large. Actually, *oocleptica* occurs in the vicinity of the only major break in the Coast Ranges of California, and an explanation of its large size is suggested by the physiography and general vegetational pattern of that region. Large size might also be the consequence of some gene flow from the Sacramento and San Joaquin valleys into the San Francisco Bay region through the break formed by Carquinez Strait. We may consider the latter hypothesis first.

If the factor of gene flow is operative and if, furthermore, it is considered the chief one in the increased size of *oocleptica*, it must be contended that the effects of this drift are manifest around both ends of the bay into Marin and San Mateo counties, respectively. The hypothesis requires, further, that the rates of modification of different characters differ and that differing degrees of selective action be responsible for these rates. Thus, color on the west side of the bay is similar to that of coastal populations to both north and south. Bill length is shorter than that of *caurina* to the north, but similar to that of *californica* to the south. Lengths of wing, tail, and tarsus are large, and differences in these dimensions between *oocleptica* and *californica* are correlated with those of body size.

Although some gene flow from the interior probably occurs, operation of this factor alone cannot provide an adequate explanation of large size in *oocleptica*. In the first place, in the latitudinal belt in which *oocleptica* makes its broadest contact with *supercilliosa*, and also to the north in the Sacramento Valley, size is somewhat smaller than to the south in the foothills of the San Joaquin Valley and in the San Francisco Bay region. This at once suggests that large size is favored in the San Francisco Bay region quite apart from the proximity of that

region to the interior valley. The less mountainous and more rolling terrain of the San Francisco Bay region is characterized by greater areas of grassland than occur to the north and south. Chaparral as an extensive vegetation type is less prevalent, but pockets and groves of broad sclerophyll forest and woodland occur in draws and canyons and also on less exposed slopes to the north and south. I am thus led to suggest that these are the critical features of the environment with which the large size of *oocleptica* is to be correlated and that in this respect there is parallelism between the environments of *oocleptica* and *superciliosa* of the foothills of the San Joaquin Valley.

The scrub jay of Santa Cruz Island, *A. c. insularis*, is strikingly larger than its mainland relatives. The similarity of *insularis* to *caurina*, *oocleptica*, *californica*, and *obscura* in all characters except large body size and proportionally larger bill indicates close relationship between them. The differences are considered to be the result of conditions peculiar to Santa Cruz Island, namely, partial occupancy by the scrub jay of a vacant predator niche together with more open physical character of the vegetation. (See discussion, p. 276.)

In the southern races of the "*woodhouseii*" group, increase in wing length is proportionally greater than that in tail length. This trend reaches an extreme in the "*sumichrasti*" group of the Sierra Madre del Sur. It is not possible to interpret these facts without precise data on the life requirements of these races. All are nonmigratory, and differences in habits which might disclose adaptive values of increased wing length, if any exist, are not known. The character of large wing among these Mexican races could be regarded as one which has undergone little change from that of the ancestral form. It may be noted that *A. c. remota*, the longest-winged race, occurs in Guerrero, the western part of the Sierra Madre del Sur, in which entire mountain range the long-winged species *A. ultramarina* is absent. It resembles *ultramarina* in characters of color of under parts and form of bill. Whether *A. c. remota* suggests *ultramarina* in behavior in any way remains to be determined; *sumichrasti* does so only in certain call notes (Pitelka, MS). While it is tempting to consider wing size along with these other characters as indicative of relationship to *ultramarina*, the exceptional wing length in these southernmost races of the *coerulescens* complex has an immediate adaptive significance irrespective of such relationship. (See footnote, p. 309.)

Interracial differences of the bill appear to be related to food habits so far as races of pine regions tend to have long, pointed, shallow, and narrow bills. This form of bill is clearly more effective as a probing device than a shorter, heavier bill. The distributional relations of the longest-billed race of the scrub jay, *nevadae*, to the piñon pine of the Great Basin have been discussed. (See p. 296.) In *A. ultramarina* the northwestern race *arizonae*, although not the largest race of that species, has the longest bill. This species as a whole occurs in woodland which usually is composed of both oaks and pines, but it would seem to me that the greater bill length in *arizonae* is indicative of some difference in the vegetation which it inhabits. This may not necessarily be a difference in the relative predominance of pines versus oaks. Conceivably, some structural feature of the cones of the species of *Pinus* in the range of *arizonae* might influence ease of extraction of the seeds, a factor which would then be selective. In the northeastern race *couchii*, the bill form is comparable to that of *arizonae*.

Jays feed primarily on a variety of insects, fruits, nuts, and seeds. This wide range in type of food vitiates most attempts to relate bill form to diet. It may be noted, however, that since mast (endosperm of pine seeds and acorns) is an important item in the diet, bill form of the races inhabiting areas in which oaks are abundant and pines are comparatively scarce might be expected to contrast with that of races of pine regions. The general heaviness of the bill of races of the "californica" group and the predominance of oaks in the Californias I regard as more than mere coincidence. A heavy bill is clearly more effective in handling acorns, particularly as a pounding tool, than a weak, small bill.

The extreme width of the bill of the Floridan race *coerulescens* is of interest in this connection. Its food habits, so far as known, do not differ from those of the Californian scrub jay (Amadon, 1944b:3). I would suggest that the reduction of bill length in this race is correlated with that in body size, and that effective mass and weight of bill have been preserved through increase in width.

There is no reason to expect that *A. ultramarina* differs from *A. coerulescens* significantly in the type of food commonly eaten. Among Mexican races of any area where both species occur, bill form corresponds closely; size of bill averages slightly smaller in all dimensions in *A. c. cyanotis* than in *A. u. sordida*, both of San Luis Potosí, but the extent of overlap in the corresponding dimensions of the two species indicates that these differences are not significant. In *A. c. sumichrasti* and *A. u. ultramarina* of Veracruz, bill size does not differ significantly. In western Texas the bill of *A. c. woodhouseii* tends to be slightly longer, but smaller in depth and width than that of *A. u. couchii*; but again there is considerable overlap in all dimensions. In *A. unicolor* the bill is proportionally heavier than in the other two species; in general it displays the form characteristic of the scrub jays of the Pacific coast.

PHYLOGENY

Speculations on the probable lines of descent of present-day forms of *Aphelocoma* rest on evidence provided by morphological characters of existing races and species and by their behavior. Relationships of the genus *Aphelocoma* to other genera of American jays must await comparative morphological studies of those genera. The fossil record of the entire group is limited to Pleistocene remains of three modern species: *Aphelocoma coerulescens* and *Cyanocitta stelleri* have been obtained at several localities in coastal southern California; *Gymnorhinus cyanocephalus* has been found in New Mexico (Wetmore, 1940).

It is likely that, of the three species, *A. unicolor* is closer to the progenitor of *Aphelocoma* than either of the other two. The basis for this suggestion is the fact that the nearest generic relatives of *Aphelocoma*, that is, *Cyanolyca*, *Cyanocitta*, and *Cissilophia*, include one or more forms which are comparably unicolored. Minor pattern differences about the head do not negate the significance of this similarity. If dark coloration is an ancestral character, it is at once implied that in these genera the lighter-colored species with white or whitish venters have arisen independently and that, therefore, mutations of an analogous, if not homologous, kind have led to parallel changes in different lines of descent. Thus one species of *Cyanocitta* (*cristata*) and two of *Aphelocoma* (*coerulescens* and *ultramarina*, possibly but not necessarily linked by one ancestral form) are light-colored.

Superficial study of the genera of American jays as well as comprehensive study of one of the genera impresses one with the fact that, from an ancestral pool of germ plasma, different potentialities and degrees of development and combinations of many essentially similar characters have been realized in different genera and species of American jays. Many intraspecific variations in one species are thus paralleled in varying degree by those of another. Examples in *A. coerulescens* and *A. ultramarina* are: dark and purplish-blue versus light and grayish-blue general coloration, relative development of pectoral collar, relative contrast of back and head, presence of shaft streaks on breast, alterations in wing-tail ratio, range of variation in size, and loss of light bill coloration before loss of juvenal plumage.

My assumption concerning the phylogenetic significance of *A. unicolor* is subject to tests by studies of comparative morphology that have yet to be made. If that assumption is accepted, the major step from *unicolor* to *ultramarina* is a change from dark to light ventral coloration. *All other features* of plumage pattern are evident, in obscure degree, it is true, but nevertheless recognizable, in *A. unicolor*. (See p. 356.) These characters are the collar pattern, throat streaking, and color contrast of back and pileum. Of the present-day races of *A. ultramarina*, the two southernmost, *ultramarina* and *colimae*, are most similar to *A. unicolor*. Size and proportions of body and extremities are similar in these forms, and the progressive differentials between adults and first-year birds in size of wing and tail are comparable. Extent of postjuvinal molt in *ultramarina* and *colimae* is less than in other races of *A. ultramarina* and is comparable to that of *A. unicolor* (Pitelka, 1945b:252). Changes in bill coloration proceed in a comparable manner in the two species (*ibid.*:256), but different rates of change are evident among races of *A. ultramarina*. Apparently, the slowest rates of change occur in the southern races *ultramarina* and *colimae*. Thus an adult male of the latter race (BS 156054, La Laguna, Jalisco), collected on March 26, 1897, had passed through at least one complete molt and therefore was at least twenty-two months old; yet the entire basal half of the mandible and the rami are yellow. In this respect the southern races of *A. ultramarina* also resemble the races of *A. unicolor*. Of the two southern races, *ultramarina* is the darker and thus is more similar to *A. unicolor* than any other race.

Within *A. ultramarina*, three groups of races are recognized. (See p. 316.) The delimitation of these groups does not necessarily imply that the differences are of a supraracial and potentially specific order; usually it serves merely to emphasize close interracial relationship. Differences between the "*ultramarina*" and "*wollweberi*" groups of *A. ultramarina* are, first, of color intensity, the dorsal blue coloration of the former being darker and brighter than that of the latter; and second, of size between the most closely neighboring races of the two groups. The latter difference raises doubt whether any genetic interchange occurs between these groups. Other differences, as of egg color, separating northern members of the "*sordida*" and "*wollweberi*" groups (see p. 316), may actually provide additional bases for group separation, but data on egg color in the southern races are not available. The "*ultramarina*" group may be distinguished from the "*sordida*"

group by the variation in bill color. The bill in the northeastern races *couchii* and *sordida* becomes black soon after departure from the nest, whereas in the southern races *ultramarina* and *colimae* the bill remains parti-colored as long as, or longer than, in races of the "*wollweberi*" group. Moreover, a surprisingly abrupt change occurs in Hidalgo between *sordida* and *ultramarina* in several characters, notably size of wing and tail. (See p. 340 and fig. 14.) Such a change is also evident in the extent of the postjuvinal molt of wing coverts (Pitelka, 1945b:252). The extent to which these two races intergrade remains to be determined, but the present evidence suggests that the amount of interbreeding, if indeed it occurs, is probably small. (See footnote, p. 341.)

Recognition of groups of races in *A. ultramarina*, and elsewhere in the genus, for that matter, is not meant to imply that intergradation between two adjacent races representing any two groups does not occur. As shown earlier (p. 317), the major contact between the "*ultramarina*" and "*wollweberi*" racial groups of *A. ultramarina*, my present skepticism notwithstanding, may occur in the southwestern part of the Mexican plateau via populations of interior Jalisco. (See p. 347.) Although few specimens are available from that area, the species is probably of fairly general distribution; vegetational maps (Sanders, 1921; Meyer, 1945) indicate that pine regions occur there.

In this connection it may be noted that retention of light coloration of the bill is a character common to the races of the "*wollweberi*" group and to the southern plateau races, with the peculiar exception of certain individuals in populations of the races *gracilis* and *wollweberi* of Zacatecas, and of one individual from interior Jalisco. Of six specimens of these races less than eight months old when collected, four have black bills and thus suggest the race *sordida*; two have parti-colored bills and thus suggest races to the north and south. Since all the remaining specimens of these races have black bills, it is evident that light coloration disappears within the first year and that the rate of change is faster than in races to the north and even more so than in races to the south. Thus these specimens suggest intermediacy in the character of bill coloration between the one extreme evident in *couchii* and *sordida* and the other evident in the southern plateau races and the northwestern races. Other questions brought up in earlier discussions, such as the geographic relations of *gracilis*, *wollweberi*, and *sordida* eastward through northern Jalisco and central Zacatecas and the relations of *gracilis*, *wollweberi*, and populations of interior Jalisco southward in Jalisco and southwestern Zacatecas, together with the problem of bill coloration outlined above, lead one to the dismaying conclusion that the best clues to the interracial relationships in *A. ultramarina* will probably be found in that part of Mexico from which, at present, the fewest specimens are available.

Although *A. ultramarina* and *A. coerulescens* are superficially similar in coloration, structural evidence indicates that the phylogenetic step from *ultramarina* to *coerulescens* is greater than that from *unicolor* to *ultramarina* and that it probably occurred before the separation of *ultramarina* and *unicolor*. Not only are modifications more numerous, but the genetic basis of some of them would seem to be more complex in the sense that each of the several characters is both qualitative and quantitative in nature and that, presumably, the genetic factors influence-

ing its expression are more numerous. The major modifications are (1) development of a collar pattern, (2) development of a superciliary line, (3) reduction in body size, (4) increase in length of tail in proportion to body size, (5) reduction of blue overcast on the sides of the head and on the back. Among the races of *A. coerulescens*, the members of the "*sumichrasti*" group, *A. c. remota* in particular, are most similar to *A. ultramarina*. These similarities are light ventral coloration, weak development of the pectoral collar, and body-wing-tail proportions, *A. c. remota* having a higher wing-tail ratio than any other race of *A. coerulescens*. The weakly developed superciliary line also suggests close relationship to *A. ultramarina*, in which this character is not developed at all.

It is possible that if these similarities have phylogenetic significance, *remota* may be more similar to the ancestral form of *A. coerulescens* than any of the other known races. The other interpretation is that the resemblances of the race *remota* and *A. ultramarina* are the result of convergence in the racial characters of *A. coerulescens* toward the species characters of *A. ultramarina* in an area which, though ecologically suitable for the latter species, is not inhabited by it. In other words, *remota* is an ecotype whose characters, at least in part, reflect evolutionary adjustment to a habitat partly taken over by a congener to the north. This latter interpretation I now prefer to the first. The close relationship of the "*woodhouseii*" group of races with the "*sumichrasti*" group is easily understood in view of the presence of connecting forms in northern Mexico.

The phylogenetic interpretation of the remaining races of *A. coerulescens* is more problematical. Dark under parts and consistently colored under tail coverts are characteristics of the races of Florida, the Rocky Mountains, the Great Basin, and Santa Cruz Island. A conspicuous collar pattern occurs in races of Florida and the Pacific coast, but the most bluish collar pattern is that of races of Florida, the Rocky Mountains, and the Great Basin. Light under parts are characteristic of Texan and Californian races. The wing is short and the superciliary line is well developed in Floridan and Californian races; but the wing is long and the superciliary line is less developed among interior races. The races of Florida, the Rocky Mountains, and the Great Basin are gray-backed and dull blue; those of Texas and California are brown-backed and bright blue. Can all these facts be reconciled? The following interpretation is offered.

It may be assumed, first, that the distribution of the scrub jay in Mexico and the Rocky Mountain region, if it has not been continuous at all times, has been disjunct, at the most, over relatively short periods. If a break actually exists at present, for example, between *cyanotis* of southern Coahuila and *woodhouseii* of western Texas (see fig. 10), this break probably has not been in existence long, in a geologic sense, as is evident from the intergrading characters of scrub jays of southern Coahuila. The same argument applies to the discontinuity in the distribution of *nevadae* and *grisea* and to the intergrading characters of *grisea* in central Chihuahua. At the northern end of this geographic continuum, *A. coerulescens* underwent differentiation to the extent that populations at the two poles of the range differed to a degree more or less comparable to that evident today. At one time the distribution of *A. coerulescens* was presumably continuous through an area now included in the Gulf states and reaching into Florida. The characters

of the Floridan jay suggest that the form then existing was dark underneath, with a well-developed collar pattern and consistently tinted under tail coverts. The separation of the western population into coastal and interior divisions leading to the differentiation of the "*californica*" and "*woodhouseii*" groups as now known occurred after the isolation of the Floridan population. In the coastal population, under parts have become light to varying degrees in different races. Correlated with this change has been a reduced frequency of tinting of under tail coverts. In collar pattern the quantity of blue is less than that evident in interior races, but the collar is more conspicuous because of the intensification of pigment, or the lightening of the venter, or both. In color of under parts the Californian races thus converge toward those of Mexico; the same is true of the more intense blue coloration and the browner back of the Californian scrub jay. In this manner, similarities of the Texan race and those of the "*californica*" group can be explained.

What remains unexplained is the puzzling geographic position of *texana* with reference to the dissimilar race *woodhouseii* to the west and the Mexican race *cyanothis* to the south, which *texana* resembles in coloration. The same is true of *grisea* in relation to *nevadae* to the north and *cyanothis* to the southeast. These incongruities between structural characters and geographic disposition of the races involved suggest some major regional shifts in populations or in gene frequencies of these populations, which have left a rather confused geographic pattern of racial characters. This is not surprising if we remember that these races evolve as ecological conditions change, and their characters do not necessarily provide clues to historical relationships of races or to the sequence of changes through time.

The character geography of interior races now suggests that the racial type represented by *woodhouseii* and *nevadae* has gradually displaced southward a type once continuous in distribution and with characters suggested by those of *texana*, *cyanothis*, and *grisea*. The parent race or race complex, originally distributed more or less continuously across the southern United States from Arizona to central Texas and southward along the Sierra Madre Oriental, is considered to have differed from *woodhouseii* and *nevadae* at least in greater length of wing and lighter coloration of venter. The degree of introgression of characters of *woodhouseii* and *nevadae* into *texana*, *cyanothis*, and *grisea* varies among both mensural and color characters, and the trends are not parallel.

The character of short wing in the Floridan and Californian race is, I believe, indicative of parallel trends in populations which live in relatively dense scrub and spend less time in flight than do interior races. Two characters peculiar to the Floridan race, namely, shaft streaks on the breast below the collar and white forehead as well as total degree of differentiation, suggest early disjunction from the population to the west. It may be noted that shaft streaks are found also in *arizonae*, the northwestern race of *A. ultramarina*, but here they are narrower and lighter. The superciliary line itself is best developed in the Californian races; the seemingly greater degree of its development in the Floridan race is probably due to the fact that the light forehead color extends posteriorly along the superciliary region; if the superciliary line was ever more conspicuous than it is in the members

of the "*woodhousei*" group, the change in forehead color has obscured that difference.

Throughout the species *A. coerulescens*, bill color of nestlings darkens rapidly, and the bill becomes entirely black before the postjuvenile molt is completed (Pitelka, 1945b:257). As noted earlier, in the northeastern races of *A. ultramarina* the bill becomes black in a comparable period of time and does not remain part-colored for varying lengths of time as it does in the remaining races of *A. ultramarina*. The similarity of *A. coerulescens* to *A. u. couchii* and *sordida* in this respect suggests another parallel evolutionary change within the history of the genus.

Lastly, it should be emphasized that the large insular form of Santa Cruz Island, *A. c. insularis*, is clearly a member of the "*californica*" group: it shares with the mainland races characteristics the differentiation of which apparently occurred subsequent to the time of disjunction of the coastal and interior populations of the scrub jay. *Insularis* differs from the mainland races primarily in size. In this character it differs from the scrub jays of the neighboring mainland to such a striking degree that the possibility of specific differentiation in this insular form is strongly suggested.

INTERSPECIFIC LIMITS

As is evident from the nomenclature adopted in this paper, the concept of species upheld here is that of the "biological" species (Mayr, 1942:119). As noted by Dobzhansky (1937:316), biological criteria of species separation do not differ from morphological criteria; rather, biological criteria are morphologic and, in addition, ecologic, behavioristic, and phylogenetic. When geographic ranges of two closely related species overlap, some kind of interspecific barrier of course exists. The problem of applying the concept of the biological species, then, is met in the delimitation, not of reproductively isolated sympatric species, but of morphologically distinct, geographically isolated, and complementary forms which may or may not represent fully differentiated species. "The decision as to whether to call such forms species or subspecies is often entirely arbitrary and subjective. . . . We cannot accurately measure to what extent reproductive isolation has already evolved" (Mayr, 1942:152).

In *Aphelocoma* the widely distributed complex of forms included under the specific name *coerulescens* well exemplifies the systematist's problem. According to earlier opinions (A.O.U. Check-list Committee, 1931:223-224; Grinnell and Miller, 1944:291), the scrub jays of Florida and Santa Cruz Island are treated as species, whereas the remaining forms of the *coerulescens* complex represent races of the species "*A. californica*," connected by intergrading populations or at least by hybridization with the production of fertile offspring. (See p. 261.) The Floridan scrub jay is clearly a morphologically distinct form; of those included in the *coerulescens* complex in this monograph, the Floridan form may be treated as a distinct species with more reason than any of the others. Differentiation of the Floridan form has progressed to so high a degree that a few structural characters are peculiar to it. Yet morphologic overlap in remaining characters points to close relationship with the western forms of the scrub jay. Available data on

behavior and habitat relations indicate that the Floridan scrub jay is essentially comparable to western forms. It is thus "equivalent" (Schmidt, 1944:255) to the western races. This view does not deny the possibility of intersterility or, what is more significant in determining specific limits, sterility of hybrids.

Grinnell and Miller (1944:291) regard "lumping" of the Floridan scrub jay with its western relatives as a "dubious guess that these two fully differentiated and widely distributed forms would interbreed if thrown together. They might react as species." This is certainly a justified contention. But when the available facts point to "equivalence," why cannot the criterion be that the allopatric forms be regarded as races of one species until further evidence indicates that some of the races are better regarded as species? In cases of the kind exemplified by *A. coerulescens* it seems to me that the onus of proof lies in the view which assumes specific distinction rather than that which assumes conspecificity. Placement of all scrub jays in one species emphasizes morphologic, behavioristic, and ecologic similarities, close phylogenetic relationship, and the fact of allopatric distribution; it unfortunately obscures the fact of advanced phylogenetic divergence of the Floridan race. Failure of two structurally similar, geographically overlapping species to interbreed, as in the example of *Dendrocopos nuttallii* and *D. scalaris* cited by Grinnell and Miller (1944:291), may result, after geographic contact, when the two forms have not proceeded farther in differentiation, *from a morphologic point of view*, than the forms placed together in *A. coerulescens*. But a comparative study of the two species of *Dendrocopos* from an ecologic point of view might well reveal some critical yet unknown factors operating to segregate the two species in addition to the factor of habitat preference. Certainly some unknown factors may exist which would prevent interbreeding between *A. c. coerulescens* and one of the western forms. We do not know. But nature has settled the question in *Dendrocopos*; here we do not *yet* know how the question was settled.

The treatment of the scrub jay of Santa Cruz Island as a race of *A. coerulescens* seems to me less subject to debate than the Floridan form. In the latter form, the level of differentiation is more or less comparable to each of the racial groups within *A. coerulescens* rather than to any single race. As a consequence, in the absence of natural or experimental proof of intersterility, specific segregation of the Santa Cruz Island form from its mainland relatives would seem to me to distort the facts of relationship which nomenclature attempts to convey. Thus Grinnell and Miller accord *insularis* specific rank, but regard the mainland races of the "*californica*" group as conspecific with those of the "*woodhousei*" group. As shown elsewhere, *insularis* is a member of the "*californica*" group, and the use of the name "*Aphelocoma insularis*" seems to me a distortion of the known facts.

Essentially, the problem here is one of objectives in our system of classification. In my opinion, recognition of more than three species in *Aphelocoma* overemphasizes morphologic distinction; recognition of three species provides a more balanced emphasis of morphologic distinctness and, moreover, does not misrepresent phylogenetic relationship. If *A. c. coerulescens* and *A. c. insularis* are accorded specific rank, it would seem to me illogical not to accord the "*woodhousei*" and "*sumichrasti*" groups specific rank also. Although *nevadae* and *superciliosa* are known to interbreed and to produce fertile hybrids, the contact between them is

TABLE 62
COMPARATIVE TAXONOMY OF GENUS APHELOCOMA BASED ON DIFFERING
SPECIES CRITERIA

Criterion of no genetic interchange or secondary contact		Criterion of potential genetic interchange	
Species	Races	Species	Races
<i>coerulescens</i> <i>woodhouseii</i>	<i>woodhouseii</i> ¹ <i>nevadae</i> <i>grisea</i> <i>texana</i> <i>cyanothis</i> ²	<i>coerulescens</i>	<i>coerulescens</i> <i>woodhouseii</i> <i>nevadae</i> <i>grisea</i> <i>texana</i> <i>cyanothis</i>
<i>sumichrasti</i>	<i>sumichrasti</i> ² <i>remota</i>		<i>sumichrasti</i> <i>remota</i>
<i>californica</i>	<i>californica</i> <i>oocleptica</i> <i>caurina</i> <i>obscura</i> <i>cana</i> <i>cactophila</i> <i>hypoleuca</i> <i>superciliosa</i> ¹ <i>immanis</i>		<i>californica</i> <i>oocleptica</i> <i>caurina</i> <i>obscura</i> <i>cana</i> <i>cactophila</i> <i>hypoleuca</i> <i>superciliosa</i> <i>immanis</i>
<i>insularis</i>			<i>insularis</i>
<i>ultramarina</i>	<i>ultramarina</i> ² <i>colimae</i> ²	<i>ultramarina</i>	<i>ultramarina</i> <i>colimae</i>
<i>sordida</i>	<i>sordida</i> ² <i>couchii</i>		<i>sordida</i> <i>couchii</i>
<i>wollweberi</i>	<i>wollweberi</i> <i>gracilis</i> ² <i>arizonae</i>		<i>wollweberi</i> <i>gracilis</i> <i>arizonae</i>
<i>guerrerensis</i> <i>concolor</i> <i>oaxacae</i> <i>unicolor</i> <i>griscomi</i>		<i>unicolor</i>	<i>guerrerensis</i> <i>concolor</i> <i>oaxacae</i> <i>unicolor</i> <i>griscomi</i>
Total, 13	Total, 23	Total, 3	Total, 30

¹ Definite secondary contact.

² Probable secondary contact.

³ Contact via interior Jalisco doubtful.

secondary, and fertility is apparently only partial. The proximity of these forms along the California-Nevada line and the sharp differences between them there strongly indicates that some isolating factors, perhaps no more than a psychic barrier, are effecting partial separation. The same is indicated by the local and abrupt character of the intergradation between *nevadae* and *superciliosa* known to occur in west-central Nevada. The contact between *sumichrasti* and *cyanotis* of the "*woodhouseii*" group is suspected to be a secondary one on the basis of, first, considerable change between these races in coloration and in size and proportions of body parts, and second, strong indications of a secondary contact in *A. ultramarina* in the same region.

The races of *A. ultramarina* are not all linked through direct, primary intergradation. Such contact is clearly shown in three separate groups: *arizonae-wollweberi-gracilis*, *couchii-sordida*, and *ultramarina-colimae*. The nature of the present-day contact between *A. u. colimae* and populations of interior Jalisco, between the latter and *gracilis*, and between *wollweberi* and *sordida* cannot be more than suggested, since many critical areas in the ranges of these races have yet to be studied. If any one of these pairs of races is now interconnected, the contacts may be of secondary origin. Contact between *gracilis* and *colimae* via interior Jalisco now seems doubtful. Contact between *sordida* and *ultramarina* in Hidalgo, if it occurs, probably represents hybridization of the kind occurring between *A. c. superciliosa* and *A. c. nevadae*. At any rate, the indication now is that this contact is also a secondary one. The races of *A. unicolor* are isolated from each other by relatively wide geographic gaps, but all are closely similar in morphological characters and, so far as known, in habitat relations.

We may now review the taxonomy of the genus *Aphelocoma* in the light of species criteria used twenty years ago and earlier by avian taxonomists and those used now. Among the forms of *A. coerulescens*, the races *coerulescens* of Florida and *insularis* of Santa Cruz Island were formerly recognized as species because direct intergradation between each of these strong differentiates and its geographically closest relative does not occur. Moreover, forms known to meet and to react so as to indicate that partial barriers exist were formerly recognized as distinct species, and many are still so recognized. Examples are such species pairs as *Colaptes cafer-auratus*, *Sturnella neglecta-magna*, *Icterus bullockii-galbula*, *Pheucticus melanocephalus-ludovicianus*, and others. Logically, then, forms or groups of forms in *Aphelocoma* between which present-day contact is secondary as well as those between which contact does not occur are to be accorded specific rank. This means that in *A. coerulescens*, not only are *woodhouseii* and its near relatives to be treated as one species, as was done formerly, but also *sumichrasti* and its near relative *remota*. Moreover, the races of *A. ultramarina*, which have always been lumped, are to be placed in two or three different species.

The species criteria just discussed, formerly favored by avian taxonomists, are those set forth in modern terms by Emerson (1945). He defines a species as "an evolved or evolving, genetically distinct, reproductively isolated natural population." This definition is intended to require that any population geographically isolated and genetically differentiated from its closest relative be recognized as a species; that is, stoppage of gene flow through geographic separation alone, with

subsequent genetic diversification, are the essential steps from race to species. If two forms with such a history meet subsequently and interbreed, as long as the contact is clearly secondary they are accorded specific rank. Mayr's (1948a:208) recent discussion of this definition indicates that he considers it more similar to his own than it really is. Mayr takes the phrase "reproductively isolated" to mean complete isolation through action of an intrinsic mechanism, whereas Emerson means mere stoppage of gene flow. In Emerson's view, as contrasted with that of Dobzhansky, Mayr, and others cited earlier, establishment of intrinsic reproductive isolation is not required as the essential step from race to species, though it is, of course, a fundamental one and usually follows those of geographic isolation and genetic differentiation. I follow the species concept of Mayr (1948a, 1949), but I realize that fundamental points concerning the speciation pattern in the genus *Aphelocoma* may be set forth by a parallel seriation of the names of the various forms according to the two sets of differing criteria. This is done in table 62. It may be added that the subjective element in the application of Emerson's definition can be avoided no more than in that of Dobzhansky and Mayr. Table 62 serves to focus attention on populations with interrelationships which are of special theoretical interest and which are worthy of further study. It also points up the fact that never in its previous history has the taxonomy of this genus been unified.

A point usually overlooked or briefly mentioned in discussions of the broader species concept of Dobzhansky and Mayr is its ecological implication. By this I refer to the fact that notwithstanding the intraspecific variability of such a species as *A. coerulescens* and the possible existence of undeterminable interracial reproductive barriers, the niche occupied by that species is approximately the same one throughout. The interracial differences, with or without concomitant evolution of intersterility, illustrate various kinds of adaptive modifications which a genetic system, fundamentally similar among all the races, permits in a niche which is fundamentally similar throughout their collective range. The races are ecotypes, comparable in broad terms to those described in plant species. (See Mayr, 1948b.) The critical turn of events in the evolution of the species comes when two closely similar forms, which are ecotypes of a widely ranging species, are brought together in a given environment. Assuming that reproductive isolation is complete and under circumstances of ecological competition, if one species is not eliminated by the other, some adaptive readjustment occurs which leads to occupation of narrower niches by the respective species or to occupation of a new niche by one of them. This is the usual turn of events that leads to the evolution of new genetic systems. Whichever species concept one applies in the genus *Aphelocoma*, the fact remains that there are fundamentally three adaptive types which meet in southeastern Mexico and occur (or did occur) in adjacent habitats. To recognize as many as thirteen species or even no more than seven or eight seems to me to be an exaggeration of the accomplishments of evolution.

I am not necessarily proposing that all closely related, geographically complementary forms which are more or less "equivalent" be regarded as conspecific. There is, for example, value in the concept of the superspecies to take care of such closely related, geographically complementary, yet morphologically divergent forms as *Cyanocitta stelleri* and *C. cristata*. One is a bird of coniferous forests; the

other inhabits deciduous forests. In my opinion, were they to occur together they would react to each other as full species. Moreover, niche relationships may be altered and a new genetic system evolved, apparently in the absence of a competitor and under circumstances of marked environmental change. An example is the adaptation of the long-billed dowitcher, *Limnodromus scolopaceus* (Pitelka, 1949), to fresh-water pond margins. Rather, the discussion here revolves about genetic versus ecologic emphasis in the species concept, and what I am proposing is that perhaps we shall be led to the latter more than we now are.

The last point requires brief explanation. In a given environment and at the community level, evolution appears to lead to increased biotic productivity with increased number of species, greater specialization to narrower niches, reduced average population levels of constituent species, with increasing integration and stabilization of the whole. We may therefore look upon the development of intersterility between well-isolated, allopatric forms, more or less concomitant with ecotypic differentiation, as merely a step which is necessary if in its subsequent history one race is to meet a congener and to occupy a given geographic area with it. Our present-day thinking about species tends to stress mechanisms of differentiation at the expense, it would seem, of the realizable products of that differentiation. Thus, Dobzhansky (1941:373) uses as the critical point in his definition of a species the stage of evolution when two previously interbreeding arrays of forms "become . . . physiologically incapable of interbreeding." Emerson (1945) uses reproductive (meaning merely extrinsic) isolation as the critical point in his definition. Here I am not raising for discussion points already adequately dealt with by Mayr (1942:119). Like Mayr, I wish to look on the species as a result rather than a stage of a process. The question is, What result do we have in mind? Let us assume that there is experimental evidence to show that the Floridan scrub jay is physiologically incapable of interbreeding with its nearest relative, the Texan scrub jay. Should it be recognized as a species even if ecologically it is a counterpart of its close congener to the west? Here I will say no, notwithstanding certain difficulties which this position faces. The basic questions to be borne in mind are these: Could the Floridan form survive as a species if it should meet its nearest relative? Or would it be eliminated? It is to these possible eventualities that I refer by the phrase "realizable products of differentiation." Therefore, from this point of view, it seems gratuitous to anticipate the outcome of evolution by recognizing species limits in genetic terms (e.g., the Floridan form as a distinct species) when in fact in ecologic terms (sympatry of that form with western races of the scrub jay) these limits have not been demonstrated and may never be so. In *Aphelocoma*, therefore, the facts are more correctly represented by the recognition of three rather than eight or nine or even thirteen species.

In the earlier discussion of phylogeny, structural modifications were identified as steps contributing to specific distinctness. The magnitude of these differences has been adequately indicated in descriptions and comparisons in earlier sections of this monograph. Interracial and interspecific differences and interrelationships are discussed there. Most importantly, it has been shown that *coerulescens* and *ultramarina*, on the one hand, and *ultramarina* and *unicolor*, on the other, are separated by morphological differences, the magnitude of most of which does

not exceed, in any evident way, that of differences separating well-differentiated races. It therefore seems to me that the theory of geographic speciation (Dobzhansky, 1937:185 ff.; Miller, 1941:374; Mayr, 1942:155) provides an adequate basis for the postulation of specific origins. The problem to which one is led from this point of view is that of synthesis of geological, paleontological, paleobotanical, and ecological evidence to determine whether it is possible to identify a sequence of events with which the facts of differentiation and distribution of the species and races of *Aphelocoma* can be correlated. Because of the magnitude of this problem, only a suggestive discussion can be undertaken at present.

DISTRIBUTION IN RELATION TO ECOLOGICAL AND HISTORICAL FACTORS

From all evidence on habitat distribution of the three species of *Aphelocoma* it may be concluded that throughout the range of each the habitat is of a more or less consistent physical structure in that certain kinds and proportions of vegetational life-forms are typically present. Natural arrays of these life-forms comprise the dominant elements in certain plant communities. Within the hierarchy of community units recognized by plant ecologists, the primary units are those defined in terms of vegetational structure, or in terms of the dominant life-forms. It is to these primary units, or formations, that the essential adjustments in habitat relations of many terrestrial birds are made (Pitelka, 1941:130). Specific differences among dominant plants of a formation, that is, differences among associations, may be reflected in minor adjustments of avian species, but those differences are rarely critical enough to determine the presence or absence of those species. When there is evidence of response to differences in plant communities of subformational rank, that response is again to life-forms or to the physical attributes of the vegetation; thus, differences among associations of the North American grassland formation or among layers of a forest community are differences in life-forms or combinations of life-forms as well as in species composition.

Strictly from the point of view of community ecology, species of *Aphelocoma* may fail to display "fidelity" in relation to any plant formation, but from the standpoint of immediate habitat relations they are constant. In the scrub jay, for example, normal activities may be confined to vegetation of a certain plant formation; or they may extend over vegetation of a comparable physical character, representing a transitional zone between plant formations of contrasting kind, or representing a successional stage within a formation the climax of which is not inhabited by the scrub jay. Thus the greater portion of the geographic range of *A. coerulescens* occupies a part of the western United States within which the chaparral-woodland complex is a predominant vegetational type, and *A. coerulescens* is characteristically associated with this vegetation. Peripherally, as along the northern California coast and the distributional tongue extending northward along the west side of the Cascades through Oregon, the scrub jay inhabits regions where a coniferous forest climax occurs; here the jay is limited to thickets and woodland borders which are chiefly of seral character.

The northern and eastern distributional limits of *A. coerulescens* coincide approximately with those of the interior woodland and chaparral formations, which

extend into southeastern Oregon, extreme southern Idaho, northern Utah, Colorado, extreme western Oklahoma, and the Edwards Plateau of Texas. Along its known northern distributional margin, *A. coerulescens* does not extend as far north as the woodland formation; thus a *Juniperus-Artemisia* association of the kind inhabited by the scrub jay in south-central Oregon occurs in central Oregon along the east side of the Deschutes River and also in southwestern Idaho (Shantz and Zon, 1924), but *A. coerulescens* does not occur in these areas. It seems probable that climatic factors, either extreme winter temperatures or persistent snow cover, or both, may limit the species to the more southern outposts of occurrence. For this ground-feeding species, the extent and persistence of snow cover may indeed be critical factors. Limitation by winter environment seems not unlikely in view of the northward projection of the geographic range west of the Cascades. In the latter region the average winter temperature is approximately 40° F., whereas in the interior the average is between 30° and 35° F. in the area where *A. coerulescens* reaches its northern limits (Kincer, 1928:4). In the Wasatch Mountains, Utah, because of the varied terrain, large areas of ground are almost continuously exposed; according to Hayward (1948:488), even after a heavy snowfall the southern and western slopes are open after a few hours or at most a few days. Here *A. c. woodhouseii* occurs in chaparral and woodland; but it presumably would be absent if the terrain were more level and the snow cover more persistent, as it is in eastern Oregon. Along the Sierra Nevada the scrub jay breeds at elevations above the average upper limits of the climax woodland-chaparral complex, but in general it does not occur above the lower part of the yellow-pine zone. The irregularity of the records at higher altitudes suggests that sporadic spread of the scrub jay upward does not result in extensive colonization, again because of the factors of winter weather.

The distribution of the scrub jay in Baja California and its occurrence there in subtropical vegetation of the lowlands in the Cape region, the mangrove swamps, and the desert scrub of the central part of the peninsula, as well as in woodland and chaparral at higher elevations, has been described. (See p. 241.) These facts seem to indicate that the scrub jay was able to invade habitats which are occupied by other species on the Mexican mainland (*Xanthoura* and *Cissilopha*); the same facts emphasize the importance of the often obscure influence of interspecific relations in determining presence or absence of members of a closely related group.

Habitat distribution of the Mexican races is, so far as is known, essentially similar to that of *A. c. woodhouseii* in the Rocky Mountains. The scrub jay has apparently occurred in the higher mountains of Mexico since its differentiation; at least one factor preventing its spread farther southeast is the lowland barrier of the Isthmus of Tehuantepec. The absence of the species in southern Jalisco and Michoacán may be related to the geographic separation of the ancestral species into divisions which gave rise to *A. coerulescens* and *A. ultramarina*. Examination of geologic, paleontologic, and biogeographic evidence from Mexico in relation to this point has yet to be made.

Restriction to particular plant formations appears to be narrower in *A. ultramarina* and *A. unicolor*. From an evolutionary point of view this is specialization in relation to habitat, and the fate of the species is more directly determined by

those environmental exigencies to which the plant formation as a unit may or may not respond. The distribution of *A. ultramarina* in Mexico is more or less coincident with that of pine-oak woodland, except that the species is absent from the Sierra Madre del Sur. Northward, *A. ultramarina* has not spread into woodland of a sim-

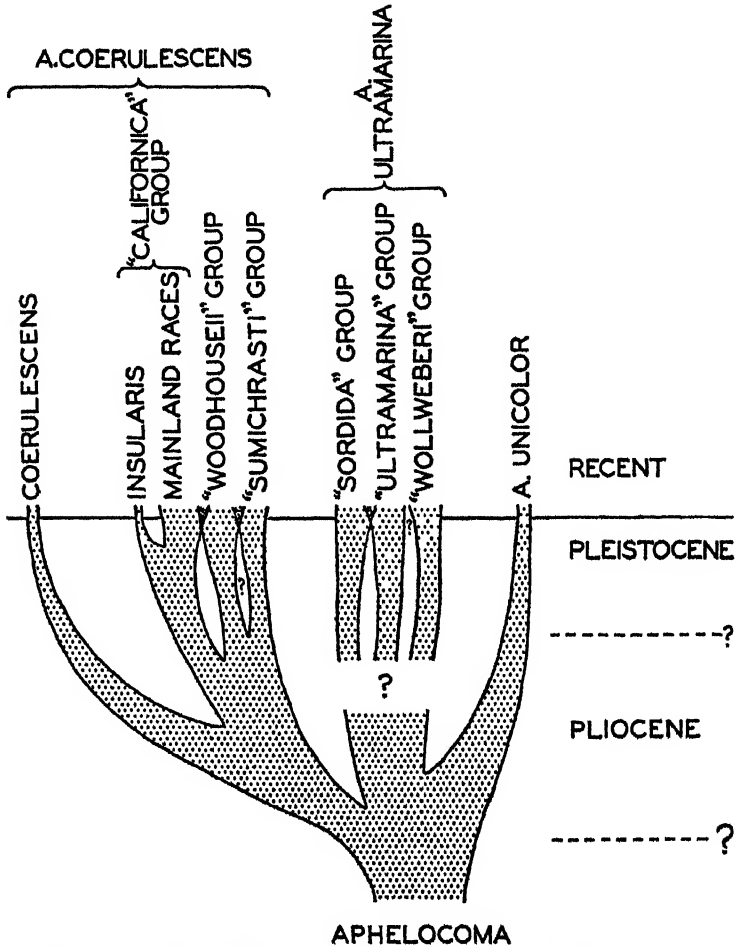


Fig. 21. Phylogeny of subdivisions of genus *Aphelocoma* suggested by available evidence; present-day contacts between various race groups considered to be secondary indicated by overlap of ends of vertical bands.

ilar character in the Rocky Mountains and the Great Basin. Although climatic factors may be critical at the northern limits of its distribution, I lean to the opinion that in these more northern areas *A. ultramarina* is replaced ecologically, in part at least, by *Gymnorhinus cyanocephalus*, which is associated primarily with piñon woodland. Like *A. ultramarina*, it is a long-winged, gregarious species prone to local wandering. *A. unicolor* inhabits temperate hardwood forests of broad-leaved and coniferous trees and, except in Guerrero and El Salvador, the upper altitudinal

borders of subtropical, Caribbean cloud forests, on the mountains of southern Mexico, Guatemala, El Salvador, and Nicaragua.

It is possible that the history of the genus *Aphelocoma* dates back to Miocene times. This suggestion is based on circumstantial evidence provided by records of historical change in physiography and vegetation which seem to correlate with several of the important evolutionary steps evident in the postulated phylogeny of the group. It must be understood that the following discussion represents only tentative views of the history of the genus. Comprehensive study of the scattered, extensive evidence which might aid in interpretations of history has yet to be made.

It may be concluded with some certainty that the derivation of the three species of *Aphelocoma* antedates the Pleistocene. Available evidence indicates that avian evolution progressed slowly in the late Tertiary and Quaternary (Miller, 1939: 807). The known remains of jays from the Pleistocene represent three modern species.

The successive glaciations of the Pleistocene must have influenced the distribution and racial differentiation of the most widely ranging species, *A. coerulescens*, in the west, but is the segregation of the "*woodhousei*" and "*californica*" groups of races of Pleistocene origin? The suggestion has been made (Dobzhansky and Epling, 1944:150, 169) that, although the pluvial periods of the Pleistocene favored the spread of piñon woodland, that spread apparently did not result in bridging the barrier of the arid regions of the southwestern desert and the western Great Basin. Presumably, then, the disjunction in the distribution of *A. coerulescens* which led to the differentiation of those groups antedates the Pleistocene and may date from the early Pliocene, when the major uplift along the Sierra Nevada and Cascade axis occurred. Before this time, distribution of the sclerophyll woodland apparently was more or less continuous in the southwest; at least, extensive desert barriers of the kind created by the uplift of the Sierra Nevada did not occur. It should be emphasized that the "*woodhousei*" and "*californica*" groups of races are the result of an east-west differentiation which does not seem to be explainable in terms of major Pleistocene events.

Differentiation of the large Santa Cruz Island form, *insularis*, occurred subsequent to separation of the "*woodhousei*" and "*californica*" groups. The fact that at least one Pleistocene connection existed between Santa Cruz Island and the mainland (Chaney and Mason, 1934:20) points strongly to the probability that *insularis* has become differentiated since the isolation of the insular population sometime in the Pleistocene. A rapid rate of change, primarily in body size, would then be indicated, and recent study of evidence from natural populations (for example, Gershenson, 1945) suggests strongly that such change may progress at considerably higher rates than has been suspected hitherto.

It is maintained by students of paleobotany that the North American vegetation attained essentially its present aspect and relative distribution by the end of the Pliocene. (See summaries by Dobzhansky and Epling, 1944:172; Axelrod, 1948.) Climatic fluctuations apparently have affected the North American biota least in the southwest, since all evidence points to a continuity in the arid environment that dates from the early Pliocene. The sclerophyll woodland with which *A. coerulescens* and *A. ultramarina* are associated spread during the Miocene, reaching southern

and central California, the Columbia plateau, and the plains region during the Miocene, and apparently became most extensive in the late Miocene and early Pliocene (Dobzhansky and Epling, *op. cit.*). Probably at this time, sclerophyll woodland extended eastward along the Gulf coast. The extension apparently existed along the southern and eastern borders of the southern Appalachian upland over a belt that has been exposed since the beginning of the Tertiary (Fernald, 1931:27). The pines and oaks of the southern states which are related to the sclerophyll woodland of Mexico apparently are derivatives of vegetation having a history in that region which dates from at least the early Pliocene. Exposure of the Florida peninsula occurred during the latter part of the Tertiary and the Quaternary. The presence of certain species of plants and animals in Florida which are isolated on the peninsula may be explained by the early eastward extension of the sclerophyll woodland. Those species represent, in part at least, segregates or relicts the separation of which from ancestral stocks is related to regional biotic shifts or fluctuations probably imposed by successive Pleistocene glaciations and the consequent southward invasions of boreal forests (Brown, 1938; Davis, 1946; Potzger and Tharp, 1947). Few concrete examples of these segregates are available, since little effort has yet been made to study the relationships of the Floridan biota to that of western North America. *A. coerulescens* is a unique example among scrub-inhabiting birds. Among plants, evidence from *Ceanothus* (Mason, 1942: 290) and *Eriogonum* and *Lygodesmia* (G. L. Stebbins, oral communication) indicates derivation of the Floridan forms from the southwest. Other good examples undoubtedly exist in different animal groups as well as plants.

It is noteworthy that the scrub jay of Florida is narrowly restricted to a xeric scrub and does not occur in pine woodland, although this vegetational type occurs in Florida; whereas the western races do inhabit woodland of similar general character. Since, therefore, this narrow ecologic restriction is peculiar to the Floridan race, it would seem to be related to events in the history of that race. Yet restriction of a parallel but less rigid kind is evident in regions where *A. coerulescens* occurs with *A. ultramarina*; in southern Arizona, for example, the former tends to be restricted to chaparral or scrub woodland, whereas the latter is characteristic of more arborescent woodland, of oaks or both oaks and pines. Available evidence indicates, however, that of the three species *A. coerulescens* probably has the widest tolerance of habitat conditions from a vegetational standpoint. The logical interpretation is therefore that in those North American areas where ecologic overlap occurs between *A. coerulescens* and any other jay (*A. ultramarina*, *Gymnorhinus*, or *Cyanocitta*, for example) *A. coerulescens* is or tends to be the scrub- or chaparral-inhabiting species, the others the woodland- or forest-inhabiting species.

Postulations on the earlier history of the genus must await further study of geologic and paleontologic records from Mexico. The following suggestive points are noteworthy, however. In the earlier discussion of phylogeny (p. 373), attention was drawn to the seemingly anomalous disposition of races in northern Mexico. It was suggested that the relationships noted between *cyanotis*, *texana*, *woodhouseii*, *nevadae*, and *grisea* might have been the result of a shift in populations or in gene frequencies. The northward spread of the sclerophyll woodland at the time of elevation of the Sierra Nevada (Axelrod, 1940) may have been followed by a range

extension involving a northward shift in the entire species over the southern Rocky Mountain states. Subsequent gradual southward restriction of some of the races or selection southwardly of the characters now found in *woodhousei* and *nevadae* could result in the separation of *texana*, *cyanois*, and *grisea*, similar in a number of characters, by the dissimilar races *woodhousei* and *nevadae*.

It is noteworthy that *A. unicolor* is an associate of the present-day remnants of the Arcto-Tertiary hardwood forest of broad-leaved and coniferous trees which spread southward in the Miocene (Dobzhansky and Epling, 1944:170). The restricted geographic range of this species, the irregularities observed in differentiation of the races (see p. 354), and comparative study of morphological characters of the genus as a whole (p. 369), all point to the conclusion that *unicolor* is a relict species perhaps derived originally from a more northern region when the Arcto-Tertiary forest was distributed extensively. It is of interest that the species occurs on the two sides of the Isthmus of Tehuantepec and that this barrier has separated the Central American temperate forests of southern Mexico and Guatemala since the middle or lower Miocene (Dobzhansky and Epling, 1944:174). Distribution of the biota of the southern temperate forest may have been continuous originally, or the highlands on the other side of the isthmus may have been colonized through sporadic transport or dispersal by various means across the barrier. Future research may determine the probable mode of spread; it seems to me that the number of Mexican avian species the distribution of which is broken by the Isthmus of Tehuantepec argues for original continuity of range. If the history of *A. coerulescens* can be dated from the Pliocene, the existence of *A. unicolor* or its direct progenitor in the Miocene seems possible. The history of differentiation of the two lighter-colored species may also go back to the Miocene if approximate timing of the segregation of the ancestral population of *A. coerulescens* into Floridan, western interior, and coastal divisions is correct. This controversial matter requires more study of evolutionary rates in animals which are members of continental or relatively old and ecologically saturated faunas.

SUMMARY

Aphelocoma is one of ten genera of American jays which form a group, possibly monophyletic, the history of which is related to that of the Mexican and Central American biota. The primary objectives of this investigation have been to determine the kind and degree of racial and specific differentiation within *Aphelocoma* and to ascertain as precisely as possible the geographic and ecologic distribution of each race and species. Additionally, data from *Aphelocoma* are presented with a view to their future use in the study of phylogeny of the American jays. Study of collections has been accompanied by field investigations of the distribution and behavior of *A. coerulescens* and *A. ultramarina* in California, Oregon, Nevada, Arizona, and Sonora.

Analyses of racial and specific differences, for which 4,817 specimens were used, are based on qualitative study of plumage characters and on statistical study of mensural characters. Segregation of age classes, bases for which were established by study of molt, is shown to be an essential step in the precise determination of racial differences and geographic trends.

Members of the genus *Aphelocoma* are nonmigratory. *A. unicolor* of the temperate cloud forests of southeastern Mexico and Central America is considered to be the oldest species, and at present consists of five relict populations each representing an isolated race. Interracial differences in color of plumage and in size and proportions of wing, tail, bill, and feet are for the most part slight and reveal no interracial trends.

A. ultramarina of the Mexican sclerophyll woodland consists of at least seven races, most of them geographically contiguous, within which three major trends of differentiation are evident. These trends are recognized through race groups, between which, according to present evidence, contact is secondary. Intergroup distinctions occur in both color and mensural characters. Within two of the race groups of parallel distribution, in the Sierra Madre Oriental and the Sierra Madre Occidental, respectively, size clines are striking and reversed.

A. coerulescens of Mexico, the western United States, and Florida, among its eighteen known races, reveals all degrees of differentiation from small intraracial variations, as in the races *californica* and *superciliosa*, to a distantly isolated race, *coerulescens*, of Florida, exemplifying an advanced stage of divergence. Small differences in general coloration or size distinguish populations or even weakly differentiated races, but these grade into significant alterations of body proportions and comparatively large differences in color, pattern, and size, which reflect usually the selective action of differential environments. Besides the isolated race *coerulescens*, the species contains three race groups. Between the "*californica*" and "*woodhousei*" groups, contact along the California-Nevada line is definitely secondary and the two complexes are partially isolated. Present evidence suggests that the contact between the "*woodhousei*" and "*sumichrasti*" groups in southeastern Mexico is also a secondary one.

In *A. coerulescens* and probably the other two species as well, most racial characters represent adjustments, through environmental selection, to regional differences in humidity and rainfall, temperature, structure and density of vegetation, or prevalent types of food.

The local distribution of *A. unicolor* partly overlaps that of *A. coerulescens*, at least in Guerrero. Such overlap, with ecological segregation, occurs in southeastern Mexico, where all three species are present. *A. ultramarina* and *A. coerulescens* are segregated ecologically in areas of geographic overlap, but *A. coerulescens* displays a wider range of ecologic distribution in areas where *A. ultramarina* is absent. *A. coerulescens* occurs in desert and tropical environments only in Baja California; in similar environments on the Mexican mainland other species of jays occur.

Characters used in determining phylogeny are plumage pattern and color, proportions, and extent of postjuvénal molt. History of the genus *Aphelocoma* is thought to date from the Miocene, when the Tertiary forests spread south into Central America. *A. unicolor* occurs in the present-day remnants of this forest. The dispersal of *A. coerulescens* in North America is apparently related to the spread of Mexican sclerophyll woodland and chaparral assemblages into southwestern North America and the Gulf and South Atlantic coastal regions in the early Pliocene. Differentiation of the northern subdivisions of *A. coerulescens* can

be correlated with the subdivision of these Pliocene assemblages by the uplift of the Sierra Nevada and the southward spread of eastern mesic forests.

Taxonomic and nomenclatural problems in *Aphelocoma* have been reviewed critically, and six heretofore unknown races have been described. These are *A. coerulescens immanis* (revived name), *A. c. caurina* and *A. c. cana*, all described herein, *A. c. nevadae* (Pitelka, 1945a), *A. ultramarina gracilis* (revived name), also described herein, and *A. unicolor oaxacae* (Pitelka, 1946a).

APPENDIX: TAXONOMY AND NOMENCLATURE

THIS APPENDIX contains synonymies of all races, data on types, and nomenclatural histories of the individual races. In addition, for each race the specimens examined are listed; where intraracial subdivisions have been accorded statistical treatment, the list of specimens is correspondingly subdivided.

In preparing the synonymies I have consulted almost all original sources, and the available literature has been sifted in order that each synonymy correctly reflect the major events in the nomenclatural history of a given race. This objective is attained, even though the synonymies have been limited to the first usage of each name, by adding citations to later papers in which the name used is the same but the concept of the race differs significantly. Variant spellings of any name published after the first usage of that name are not included.

Nomenclatural histories were written for individual races, at first, in an effort to organize and summarize the abundant literature on the many members of this genus. They now serve as a partial background for nomenclatural changes adopted in the course of my studies. In many instances these histories serve to unravel otherwise involved chronological series of nomenclatural usages by a number of different systematists. The objective is not to report merely successive events in the nomenclatural history of the genus, but to present a comprehensive critical review of that history.

Genus *Aphelocoma* Cabanis

Garrulus, Vieillot (1817:476), part.

Pica, Wagler (1827:sp. 11), part.

Corvus, Bonaparte (1828a:58), part.

Cyanurus Swainson and Richardson (1831:496), part.

Cyanocorax, Bonaparte (1838:27), part.

Cyanocitta Strickland (1845b:342), part; Baird (1858:584, not of Strickland); Amadon (1944a:6, not of Strickland or Baird), part.

Aphelocoma Cabanis (1851:221), original description; type, by subs. desig. (Baird, 1858:584),

Garrulus californicus Vigors; Sharpe (1877:112, not of Cabanis), part.

Garrulina J. E. Gray (1855:148), type, by orig. desig., *Cyanocorax unicolor* Du Bus, part. (*Garrulina* Bonaparte, 1854:113, is a *nomen nudum*.)

Sieberocitta Cones (1903:497, 499), type, by monotypy, [*A.*] *sieberi arizonae* Ridgway [= (Baird and Ridgway)], part.

No attempt is made in this paper to discuss the nomenclatural history of the generic category *Aphelocoma*, since the necessary research involves a thorough study of related genera which figure in the above synonymy as well as others. (See p. 203.) Taxonomic changes proposed by Amadon (1944a) in his survey of the genera of Corvidae may prove to be sound; but until comprehensive comparative studies of structure have provided the necessary foundation for satisfactory interpretations of phylogeny, it seems best to retain most of the generic categories recognized by Ridgway (1904) and Hellmayr (1934). Amadon (1944a) proposed a wholesale lumping of four American genera, *Cyanocitta*, *Aphelocoma*, *Cissilopha*, and *Cyanolyca*. I do not deny the possibility that, among these, *Cyanocitta* and *Aphelocoma* are more closely related than any other two of the four, and future research might favor combination of these two genera. But use of *Cyanocitta* for

the species of *Aphelocoma* at this time would seem to me to support the use of Amadon's more inclusive category, an action for which adequate data are not available.

***Aphelocoma coerulescens californica* (Vigors)**

- Corvus ultramarinus* (not of Bonaparte), Audubon (1838:456).
Garrulus californicus Vigors (1839:21), original description.
Garrulus ultramarinus (not of Temminck), Audubon (1839:154), part.
Cyanocitta californica, Strickland (1845b:342), part.
Cyanocorax californicus, Gambel (1847:201).
[Garrulus] palliatus, Drapiez (in Bonaparte, 1850:377, in synonymy).
A[phelocoma] californica, Cabanis (1851:221).
Corvus palliatus Drapiez (in Bonaparte, 1853:828, in synonymy).
Garrulus floridanus (not *Corvus floridanus* Bonaparte), Schlegel (1867:64), part.
[Cyanurus] californicus, Gray (1870:4).
Cyanocitta floridana, Allen (1871:298), part.
[Aphelocoma floridana] var. californica, Coues (1872:166), part.
[Aphelocoma floridana var. woodhousei] c. californica, Coues (1874b:219), part.
[Cyanocitta californica] var. californica, Baird, Brewer, and Ridgway (1874:284), part.
Aphelocoma californica californica, Grinnell (1902:45), part; Ridgway (1904:327, not of Grinnell), part; Swarth (1918:410, not of Grinnell or Ridgway), part.
Aphelocoma coerulescens californica, Hellmayr (1934:52), part.

Type.—Taken at Monterey, Monterey County, California; type specimen probably nonexistent (Grinnell, 1932:287).

Nomenclatural history.—As defined at the turn of the century, the race *californica* ranged over California west of the Sierra Nevada and south to at least the Coast Ranges in the vicinity of Los Angeles. Except for the southern portions of this area, no major change occurred in the nomenclatural status of *californica* until 1918, when Swarth redefined *immanis* of Grinnell (1901) from Oregon as a larger, paler race extending southward into the central valley, and described as new *oocleptica*, a large race, similar in color to *californica*, from the San Francisco Bay region and the northern California coast. The greater part of his material came from the San Francisco Bay region, and figures on size which he published (1918: table facing 422) were based on specimens from Marin County. The presence of this large coastal race in the San Francisco Bay region has been confirmed by my own studies (see p. 219), but specimens from the northern coast are smaller than *oocleptica*, *sensu stricto*, and represent a dark race of size comparable to that of *californica*. The northern race *caurina* is newly named in this paper (p. 225).

Of the several early names applied to the California scrub jay, only one needs special comment: "*Corvus palliatus* Drapiez," listed by Bonaparte (see synonymy), and among American authors by Baird, Brewer, and Ridgway (1874:288) and Coues (1874b:219), was later dropped by Ridgway and other authors, presumably because the identity of the name could not be established definitely or because, so far as known, it was only a manuscript name, or for both reasons. The type of Drapiez's *palliatus* was examined by A. J. van Rossem in 1933 at the Brussels Museum. He has kindly provided me with the following data: Type, Brussels Museum no. 5246B; wing, 120 mm.; tail, 133 mm. (central pair of rectrices missing); bill length (from nostril), 21.5 mm.; tarsus, 37.2 mm. "Mounted bird in very

bad condition. . . No sex indicated, but definitely a bird of the year as shown by narrow rectrices and first-year primaries. Plumage fresh, . . . just completed first fall molt. This specimen is identical in coloration with 3 specimens from 'San Francisco' [in the Brussels Museum] but all are badly faded and not of much value. I should estimate it to be *californica*, however. Under parts very pale. Under tail coverts . . . grayish white, that is not bluish" (van Rossem, letter).

The name *palliatatus* has been cited several times in the synonymy of *californica*; since van Rossem has established its identity it should be restored to the nomenclatural record of that race. Although the possibility remains that additional information concerning this name, as place of publication and type locality, may be unearthed some day, it apparently cannot be used other than as a substitute for *californica* (Peters, 1934: 315 n.).

Specimens examined.—Total, 277, divided as follows: (1) outer coastal central California, from Santa Cruz County to San Luis Obispo County, 116 (table 4); (2) inner coastal central California, from Santa Clara and Alameda counties south to San Luis Obispo County, 116 (table 6); (3) Santa Barbara and Ventura counties, 45 (table 7).

1) *Santa Cruz County*: 1 mi. N Bonnie Doon (1,900 ft.), 1; 1½ mi. S Bonnie Doon (800 ft.) 1; Boulder Creek, 2; Mount Hermon, 1; Santa Cruz, 5. *Monterey County*: Big Creek (Lucia P.O.), 1; headwaters, Big Creek, 1; Big Sur River, 1; 2 mi. E Bryson, 3; 1½ mi. S Chalk Peak (3,000 ft.), 1; 7 mi. SE Del Monte, 3; 1½ mi. S Marina, 1; 3 mi. NNE Natividad, 1; Pacific Grove, 1; 20 mi. S Pacific Grove, 1; Partington Point, 2; Robinson Canyon (Carmel Valley), 1; 4 mi. NE Salinas, 1; Santa Lucia Range: head of Cares Trail (4,600 ft.), 1, China Camp, 2, Santa Lucia Peak (5,600 ft.), 1, head of Calaboose Creek, 1; Monterey (type locality, and including Del Monte, Seaside, and Carmel), 66. *San Luis Obispo County*: Morro, 6; 4 mi. S Morro 2; Nacimiento River (1,250 ft.), 5; Paso Robles, 1; San Carpojo Creek (7 mi. N Piedras Blancas), 3.

2) *Santa Clara County*: Berryessa, 1; Calaveras Valley, 1; College Park, 3; Los Gatos, 6; Mount Hamilton, 1; San Jose, 2; unspecified, 1. *Alameda County*: Cedar Mountain, 1. *San Benito County*: Bear Valley, 2; Bickmore Canyon (1,700 ft., 4 mi. NW Pinnacles P.O.), 1; Cook P.O. (Bear Valley, 1,300 ft.), 2; 4 mi. S Hernandez (4,000 ft.), 2; Mulberry, 1; 2 mi. NNE New Idria (1,900 ft.), 3; 2 mi. SE Panoche (1,200 ft.), 1; Panoche Pass, 1; Paicines, 11; 4 mi. NNE San Benito, 5; 6 mi. ESE San Benito (1,600 ft.), 7; 1 mi. SE summit, San Benito Mountain (4,400 ft.), 3. *Monterey County*: Abbott Ranch, Arroyo Seco, 1; Jolon, 7; 2½ mi. N Lockwood, 1; Paraiso Springs (1,400 ft.), 5; Priest Valley, 3; San Lorenzo Creek (Peachtree Valley, 1,475 ft.), 2; San Lucas, 1; 1½ mi. S Soledad (183 ft.), 4; 4 mi. S Soledad, 1. *San Luis Obispo County*: Cammatti Creek (1,650 ft.), 18; 3½ mi. E, 1½ mi. N McChesney Mountain (1,900 ft.), 3; San Juan River, 4½ mi. ENE La Panza, 1; San Miguel, 7; 4 mi. S, 5 mi. E Shandon (1,175 ft.), 5. *Fresno County*: Waltham Creek (4½ mi. SE Priest Valley, 1,850 ft.), 2.

3) *Santa Barbara County*: Buellton, 4; Guadalupe Lake, 3; Lompoc, 9; Point Conception, 3; Santa Barbara, 6; Santa Ynez River, 3. *Ventura County*: Cañada Larga, 1; Ojai Valley, 7; Pine Creek, 1; head of Piru Creek, 2; Santa Paula, 5; Ventura, 1.

Aphelocoma coerulescens oocleptica Swarth

Cyanocitta californica, Newberry (1857:85), part.

Aphelocoma californica, Sharpe (1877:118), part.

Aphelocoma californica californica, Grinnell (1902:45), part.

Aphelocoma californica oocleptica Swarth (1918:413), original description, part.

Aphelocoma coerulescens oocleptica, Hellmayr (1934:51), part.

Type.—First-year male, no. 7128, MVZ; Nicasio, Marin County, California; collected by Walter P. Taylor, February 23, 1909; orig. no. 647. Blue coloration of

the type is paler and duller than that of adult males taken at the same time of year; that of the crown, nape, and sides of head is less purplish. Plumage worn slightly; margins of tail feathers worn terminally, except four on the right side which are replaced. Scattered feathers on sides of back are markedly worn and faded terminally; these are apparently feathers held over from the juvenal plumage. Measurements (mm.): wing, 128.4; tail, 132.8; bill length, 18.8; tarsus, 41.7.

Nomenclatural history of the race *oocleptica* has been discussed in conjunction with *californica*.

Specimens examined.—Total, 323, divided as follows: (1) Marin County and the San Francisco peninsula, 115 (table 8); (2) southwestern Solano County, central Contra Costa County, and Alameda County, 130 (table 9); (3) northwestern Santa Clara and southeastern San Mateo counties, 78 (table 10).

1) *Marin County*: Fairfax, 1; Inverness, 7; 3 mi. W Inverness, 1; 5 mi. W Inverness, 1; 5 mi. NW Inverness, 8; 2 mi. NE Inverness, 1; Mailliard (= Woodacre), 10; Marshall, 1; Mount Tamalpais, 2; Nicasio, 27 (including type); Olema, 1; Point Reyes Station, 1; San Geronimo, 42; San Rafael, 1; Tomales Point, 3; unspecified, 2. *San Francisco*: Golden Gate Park, 2. *San Mateo County*: Baden, 4.

2) *Solano County*: 4 mi. NE Benicia, 3; Cordelia, 1; 3½ mi. SW Cordelia, 2; 4 mi. S Cordelia, 1. *Contra Costa County*: Alhambra, 1; Cowell, 1; Danville, 5; 1 mi. N Lafayette, 1; 2½ mi. SE Lafayette, 1; 1½ mi. W Lafayette, 1; Las Trampas Creek, 1; Moraga, 1; 3 mi. NE Moraga, 1; Moraga Valley, 8; Orinda, 1; Pacheco, 2; 2 mi. SW Walnut Creek, 4; 2½ mi. SE Walnut Creek, 1; unspecified, 1. *Alameda County*: Alameda, 10; Berkeley, 23; Calaveras Dam, 1; Eden township (near Hayward), 6; Hayward, 39; Oakland, 11; unspecified, 3.

3) *Santa Clara County*: Los Altos, 4; Mayfield, 2; Palo Alto, 56. *San Mateo County*: Atherton, 1; Menlo Park, 6; Ravenswood, 1; Redwood City, 2; Woodside, 1; southeastern San Mateo County, 5.

***Aphelocoma coerulescens caurina* Pitelka**

Cyanocitta californica, Baird (1858:xliii, 584), part.

Garrulus floridanus (not *Corvus floridanus* Bonaparte), Schlegel (1867:64), part.

Aphelocoma californica, McGregor (1896:130).

Aphelocoma c[alifornica] californica, Mailliard (1916:199).

Aphelocoma californica oocleptica Swarth (1918:413), part.

Aphelocoma coerulescens oocleptica, Hellmayr (1934:51), part.

Aphelocoma coerulescens caurina Pitelka, original description, see page 225.

Type.—See page 225.

Nomenclatural history of the race *caurina* has been discussed in conjunction with *californica*.

Specimens examined.—Total, 169 (table 11). **CALIFORNIA**. *Sonoma County*: 8 mi. E Cloverdale, 1; Freestone, 1; Fulton, 1; Guerneville, 10; Healdsburg, 13; 3 mi. NNE Kellogg, 1; Monte Rio, 9; Petaluma, 2; Santa Rosa, 2; Sebastopol, 2; Sobre Vista, 1; Sonoma, 1; Stony Point, 2; Wheatfield Fork, Gualala River (265 ft.), 1. *Napa County*: Angwin (Howell Mountain), 1; Mount St. Helena, 5; Mount Veeder, 1; unspecified, 1. *Lake County*: Castle Hot Springs, 8; Glenbrook, 2; Harbin Hot Springs, 3; Lower Lake, 1; 6 mi. NE Middletown, 8; 5 mi. E Upper Lake, 1. *Mendocino County*: Bald Hill, 1; Cahto, 1; Cummings, 1; Hearst P.O., 3; 6 mi. SW Laytonville, 1; Lierly's, 1; Miller (near Elk), 1; Mendocino City, 1; Mount Sanhedrin, 3; Sherwoods, 3; Westport, 1. *Trinity County*: 2 mi. E Hayfork, 7; Helena, 1; 1 mi. W Hyampom, 3; 2 mi. W Hyampom, 3; 1 mi. NW Mad River Bridge (2,300 ft.), 1; Peanut, 1; Ruth, 2; 7 mi. W Ruth, 1. *Humboldt County*: 2 mi. NE Arcata, 1; Bluff Creek, 3; 4 mi. NE Bridgeville, 3; Carlotta, 1; Coyote Peak, 1; Eureka, 2; Hoopa Valley, 1; Kneeland, 5; Maple Creek (1 mi. N Mad River junction), 3; Petrolia, 1; Redwood Creek (800 ft.), 3; Schoolhouse Peak, 1; 2 mi.

NW Thompsons, 1; $1\frac{1}{2}$ mi. S, $\frac{1}{2}$ mi. E Willow Creek (600 ft.), 2. Del Norte County: Patrick Creek, 2; $6\frac{1}{2}$ mi. E Smith River (1,000 ft.), 2.

OREGON. Curry County: Brookings, 2; Pistol River, 2; Wedderburn, 1; 1 mi. E Wedderburn, 18 (including type).

Aphelocoma coerulescens obscura Anthony

Cyanocorax californicus, Heermann (1853:269), part.

Cyanocitta californica, Baird (1858:584), part.

[*Aphelocoma floridana*] var. *californica*, Coues (1872:166), part.

[*Aphelocoma floridana* var. *woodhousei*] c. *californica*, Coues (1874b:219), part.

Aphelocoma californica, Ridgway (1881:30), part; Bryant (1889b:293, not of Ridgway), part.

Aphelocoma californica obscura Anthony (1889:75), original description; Ridgway (1904:330, not of Anthony).

Aphelocoma californica californica, Grinnell and Swarth (1913:261), part; Swarth (1918:410, not of Grinnell and Swarth), part.

Aphelocoma coerulescens obscura, Hellmayr (1934:52), part.

Type.—Adult male, no. 17156, C; Valladeres, 2,700 feet, west base of the Sierra San Pedro Mártir, Baja California, Mexico; collected by A. W. Anthony, September 8, 1888; orig. no. 2543. My measurements of the type are as follows (mm.): wing, 125.8; tail, 145.6; bill length, 21.6; bill depth, 8.7; tarsus, 38.3.

Nomenclatural history.—Considerable difference of opinion has existed about the status of the race *obscura*, first, in regard to its own validity, and second, in regard to its distributional relations with *californica*. Although the A.O.U. nomenclatural committee recognized *obscura* in 1890, Anthony (1893), who described this race in 1889, himself doubted its validity on the basis of similarities between specimens from the Sierra San Pedro Mártir and others from San Diego County, then regarded as "*Aphelocoma californica*" (A.O.U. Check-list, 1895:197). Anthony's suspicions proved to be well founded, but jays of both regions were regarded by other ornithologists as separable from the race *californica*; and subsequent authors extended the range of *obscura* northward to include the southern California coast north to Los Angeles (Grinnell, 1898:31; Ridgway, 1904:330; A.O.U. Check-list, 1910:225; Oberholser, 1920:91). But over most of the time spanned by these publications and later, scrub jays of the southern coast, as often as not, were considered indistinguishable from *californica* (Grinnell, 1902:45, 1908:84; Willett, 1912:67; Todd, 1928:355; A.O.U. Check-list, 1931). The question was first discussed in a critical manner by Grinnell and Swarth (1913:261), who held that there was no perceptible difference in size—mass or proportions—or in color of specimens from the San Jacinto area and from the central coast of California. They held that the race *obscura* did not occur in California, but lacked specimens from the Sierra San Pedro Mártir to evaluate its status there. In 1918 Swarth reaffirmed this interpretation of the race *californica*, extending its known range southward over the Sierra San Pedro Mártir, and reducing *obscura* to a synonym of *californica*. But Swarth (1918:410) lacked fresh-plumaged specimens of *obscura*; after additional material from critical areas became available, both Swarth and Grinnell agreed that *obscura* was a valid race (Huey, 1926:355; Grinnell, 1928:146).

Obscura is a well-marked race. Its distributional limits north of the Sierra San Pedro Mártir have been defined here on the basis of a large series of specimens from southern California. In discussing intergradation (p. 234) I have presented

data to show that, in color as well as size, specimens from San Diego County are clearly referable to *obscura*. Over a rather broad belt of intergradation northward with *californica*, specimens as far north as the Los Angeles area prove to be closer to *obscura* than to *californica*. The present use of the name *obscura* is thus similar to that of Ridgway (1904:330). Swarth's data (1918: table facing 408) show little difference in size among his several samples of "*californica*" because he did not segregate first-year specimens from adults. I have examined most of the material he had, and have found that his sample from the "Santa Cruz" region, representing typical *californica*, was made up chiefly of first-year specimens; the single specimen listed as a typical example of color characters (Swarth, 1918:410, MVZ 7016) is a first-year male.

Specimens examined.—Total, 547, divided as follows: (1) Ventura, Los Angeles, southwestern San Bernardino, Orange, and western Riverside counties, 258 (table 14); (2) San Diego County and extreme northern Baja California, 155 (table 13); (3) northern Baja California, chiefly the Sierra San Pedro Mártir, 134 (table 12).

1) *Ventura County*: Simi, 2; Simi Hills (NW end Chatsworth Tunnel), 1. *Los Angeles County*: Azusa, 1; Altadena, 7; Calabasas, 3; Covina, 1; Glendora, 2; Highland Park, 2; Lankershim, 3; Los Angeles, 11; Mint Canyon (2,400 ft.), 3; Monrovia, 2; Mount Markham (5,500 ft.), 2; 5 mi. E Palmdale, 1; Pasadena, 82; Pomona, 2; Puente, 1; San Fernando Valley: Los Nogales, 5, San Fernando, 3, Tujunga Wash, 1, and unspecified, 1; San Francisquito Canyon, 1; San Dimas, 2; San Gabriel Mountains: Chleno, 1, Hennigers Flat, 1, and San Gabriel Canyon, 1; Santa Monica Mountains, 10; Caluenga Pass (Santa Monica Mountains), 6; Saugus, 1; Sawtelle, 2; the Sierra Madre: Dark Canyon, Arroyo Seco, 1, Mount Wilson, 1, and Switzer's Camp, 1; 5 mi. W Shoemaker, 1; Verdugo, 2; Verdugo Canyon (N of Glendale), 1; unspecified, 2. *Orange County*: Laguna Beach, 1; Trabuco Canyon (1,700 ft.), 2. *San Bernardino County*: Cajon Pass (4,000 ft., coastal side), 3; Camp Baldy, 1; 7 mi. NW Colton, 1; Hesperia, 1; 9 mi. W Hesperia, 1; Redlands, 20; 4 mi. SE Redlands, 2; Reche Canyon (near Colton), 3; Quail Spring (3,600–4,500 ft.), 10; San Antonio Canyon, 3; San Bernardino Mountains: Bluff Lake (7,400–7,500 ft.), 2, Cactus Flat (6,000 ft.), 1, Doble (7,000 ft.), 1, Foresee Creek (5,000 ft.), 1, and unspecified, 1; Summit, 1. *Riverside County*: Beaumont, 2; Covington Flat (Joshua Tree National Monument, 4,500 ft.), 1; Little San Bernardino Mountains: Live Oak Spring, 1, Little Oak Spring, 1, and Pinyon Wells (4,000 ft.), 6; San Jacinto, 2; San Jacinto Mountains: Hemet Lake (4,400 ft.), 4, Kenworthy (4,500 ft.), 5, Schain's Ranch (4,900 ft.), 4, and unspecified, 2; Santa Rosa Mountains (Dos Palmas Springs, 3,500 ft.), 1; Riverside, 3; Valle Vista (1,800 ft.), 1.

2) CALIFORNIA. *San Diego County*: 3 mi. W Boulevard (3,500 ft.), 2; 8 mi. W Boulevard, 1; Carlsbad, 1; Campo, 3; Cuyamaca Mountains, 5; Dehesa, 3; Descanso, 1; Dulzura, 3; Escondido, 2; 5 mi. NE Escondido, 3; Fliinn Springs, 2; 6 mi. N Foster, 2; 4.5 mi. NW Hot Springs Mountains, 2; Jacumba, 15; Julian, 5; Laguna Mountains (5,500 ft.), 1; Lakeside, 1; Los Peñasquitos Ranch, 1; Mesa Grande, 1; Mission Dam, 5; Pala, 1; Palomar Mountain, 1; Poway, 5; Ramona, 6; Rose Canyon (100 ft.), 2; San Diego, 9; San Marcos, 6; Santee, 2; 5 mi. N Santa Ysabel, 1; Volcano Mountains, 3; Wagon Pass (Coast Ranges, 3,500 ft.; see Mearns, 1907:133), 1; Warner Pass, 1; Witch Creek, 29.

BAJA CALIFORNIA. N side Descanso Bay, 1; N end Nachoguero Valley (3,400 ft.), 14; Ojo (Nachoguero Valley, 3,429 ft.), 9; Tanama, 1; Tecate River (SE Tecate Mountain, 1,700 ft.), 4.

3) BAJA CALIFORNIA. Agua Hedicerera (32°30' N, 116°16' W), 1; 10 mi. SE El Alamo, 17; El Piñon, 4; El Rayo, 7; El Valle de la Trinidad, 6, and (at 2,500 ft.), 1; Ensenada, 1; Las Cabras, 1; Las Cruces (2,600 ft.), 5; Ojos Negros, 1; Rancho Santo Tomás, 5; San Antonio Ranch (upper Río Santo Domingo, 2,100 ft.), 4; San Fernando (1,100 ft.), 1; San José (2,500 ft., 31° N), 8; San Matías Pass, 1; Sierra San Pedro Mártir: Concepción (6,000–6,200 ft.), 10, La Grulla, 8, La Jolla (6,200 ft.), 3, Santa Eulalia (8,000 ft.), 6, Santa Rosa Flat, 2, Valladeres Creek (2 mi. S La Jolla), 4, Vallecitos (7,500–8,500 ft.), 4, and unspecified, 7; Sierra Juárez: Laguna Hanson (5,200 ft.), 17, 30 mi. N Laguna Hanson, 1, and Los Pozos (4,200 ft.), 6; Valladeres (2,700 ft.), 3 (including type).

***Aphelocoma coerulescens cana* Pitelka**

Aphelocoma coerulescens cana Pitelka (see p. 237), original description.

Type.—See page 237.

Nomenclatural history.—To my knowledge there are no previous records of the scrub jay from the range now attributed to *cana*.

Specimens examined.—Total, 4. CALIFORNIA. *Riverside County*: Eagle Mountain (4,000–4,200 ft.), 3 (including type). BAJA CALIFORNIA. 3 mi. W Alaska (3,500 ft.), 1.

***Aphelocoma coerulescens cactophila* Huey**

Aphelocoma californica hypoleuca, Bryant (1889a:24), part.

Aphelocoma californica californica, Swarth (1918:410), part.

Aphelocoma californica obscura, Thayer and Bangs (1907:138), part.

Aphelocoma coerulescens hypoleuca, Hellmayr (1934:53), part.

Aphelocoma californica cactophila Huey (1942:43), original description, part.

Aphelocoma coerulescens cactophila, A.O.U. Check-list Committee (1945:445), part.

Type.—Adult female, no. 13549, SD; three miles north of Punta Prieta, Baja California, Mexico (lat. 28°56' N, long. 114°12' W); collected by Laurence M. Huey, October 24, 1930. Huey's measurements (1942:444), in millimeters, are: wing, 114.5; tail, 125.2; tarsus, 37.5.

Nomenclatural history.—In 1889 Bryant reported for the first time the occurrence of scrub jays north of the Cape region of Baja California, along the Pacific coast from Magdalena Bay northward to latitude 28°. From that time until 1942, scrub jays of the waist of the Baja California peninsula had been regarded as representative of the race of the Cape region, *hypoleuca*. In 1942 Huey described the scrub jays of central Baja California as a smaller, darker race, *cactophila*, ranging from latitudes 29°20' to 25°40'. As redefined here, *cactophila* ranges over a larger area; it is smaller than *hypoleuca*, as shown by Huey, but duller, not darker, than that race.

Specimens examined.—Total, 98 (table 15). *North District*: Calmallí, 2; 10 mi. W El Cañon, 2; Mesquitán, 2; 30 mi. SE Mesquitán, 1; 3 mi. N Punta Prieta (type locality), 1; 9 mi. N Punta Prieta, 1; 25 mi. N Punta Prieta, 6; San Andrés, 1; San Borjas, 1; Santana, 2; 5 mi. N Santa Rosalía Bay, 2; 10 mi. W Santa Rosalía, 3; 24 mi. W Santa Rosalía, 1; Santa Teresa Bay (28°20' N, Gulf side), 4; Yubay, 4.

South District: 2 mi. N San Bruno, 2; 15 mi. S Campo Alemán, 1; Campo Los Angeles, 1; Concepción Bay, 2; S end Concepción Bay, 2; El Refugio, 1; Loreto, 1; 10 mi. N Los Angeles, 1; Magdalena, 1; Magdalena Bay, 8; N lagoon, Magdalena Bay, 10; Mulegé, 1; San Ignacio (27°17' N), 9; San Jorge, 9; San Bruno, 1; Llano de San Bruno, 8; San Lucas (12 mi. S Santa Rosalía), 5; Santa María Bay (near Magdalena Bay), 2.

***Aphelocoma coerulescens hypoleuca* Ridgway**

Cyanocitta californica, Baird (1859a:301), part.

[*Aphelocoma floridana*] var. *californica*, Coues (1872:166), part.

Aphelocoma californica, Ridgway (1881:30), part.

[*Aphelocoma*] *californica hypoleuca* Ridgway (1887:356), original description.

Aphelocoma hypoleuca, Swarth (1918:420).

Aphelocoma coerulescens hypoleuca, Hellmayr (1934:53), part.

Type.—Adult male, no. 86325, USNM (Grinnell, 1928:147); La Paz, formally designated as type locality by Ridgway (1904:331); collected by L. Belding, December 18, 1881. My measurements of the type are as follows (mm.): wing, 122.8; tail, 137.7; bill length, 19.6; bill depth, 9.7; tarsus, 40.1.

Nomenclatural history.—Baird, Brewer, and Ridgway (1874:288) first described specimens of scrub jays from Cape San Lucas as being smaller and whiter than what was then regarded as typical *californica*. Later, Ridgway (in Belding and Ridgway, 1883a:541) noted differences of lighter under parts and white under tail coverts. It was not until 1887, however, that Ridgway recognized jays of the Cape region as a separate race under the name *hypoleuca*. Brewster (1902:124) defined the characters of this race in greater detail, although two of the proposed differences, that *hypoleuca* is "considerably smaller" and bluer on sides of head than *californica*, are without basis. Swarth (1918:221) properly suggested that the supposed size difference was "probably due to comparisons being made with a series of the form *immanis*" (now *superciliosa*). Actually, there is a slight difference in the direction suggested by Brewster (see tables 4 and 16); *hypoleuca* is not larger than *californica*, as stated by Swarth, whose series of the latter from the central coast of California was made up mostly of first-year birds.

Swarth (1918:420) argued for specific distinctness of *hypoleuca*, pointing to the separation of *hypoleuca* from the only other race approaching it in paleness, "*immanis*" (= *superciliosa*), by the darker "*californica*" (including *obscura*). As a further basis for his decision, Swarth held that there was an abrupt change in appearance from *californica* to *hypoleuca*; he lacked material, however, from the waist of the peninsula, although a number of records from that area were available in the literature up to 1917 (Bryant, 1889a:24, 1889b:293, cited by Bendire, 1895:378, and Brewster, 1902:125). Soon after the appearance of Swarth's paper, Oberholser (1918b) published new records of *hypoleuca* north of the Cape region to Yubay (29°20' N) which bridged the supposed break, structural and geographic, between the two Baja Californian races as defined by Swarth. An actual gap in the distribution of scrub jays occurs north of Yubay. Swarth's *hypoleuca* is equivalent, however, to the race *hypoleuca*, *sensu stricto*, as here recognized.

Specimens examined.—Total, 153 (table 16). Agua Caliente (700–800 ft.), 9; El Oro, 1; El Sauz (4,000 ft.), 7; El Valle, 9; Frailes Bay, 1; La Laguna (5,500 ft.), 1; La Paz, 43 (including type); Miraflores (600 ft.), 7; 7 mi. S Miraflores, 4; Muertes Bay, 1; 7 mi. NW San Bartolo, 4; San Bernardo Mountains, 1; San Lucas (at Cape San Lucas), 22; 9 mi. E Cape San Lucas, 2; San José del Cabo, 16; San Nicolás, 1; Santa Anita, 1; Santiago, 2; Sierra de la Laguna (northern Victoria Mountains), 10; Todos Santos, 4; Triunfo, 7.

***Aphelocoma coerulescens superciliosa* (Strickland)**

Cyanocitta superciliosa Strickland (1845a:260), original description, part.

Cyanocitta californica, Strickland (1845b:342), part.

Cyanocorax californicus, Heermann (1853:269), part.

Cyanocitta floridana, Allen (1871:298), part.

Cyanocitta floridana var. *californica*, Ridgway (1874:172), part.

Aphelocoma floridana var. *californica*, Nelson (1875:360), part.

Cyanocitta var. *californica*, Henshaw (1877:1304), part.

Aphelocoma californica, Belding and Ridgway (1879:422), part.

Aphelocoma californica californica, Grinnell (1902:45), part.

Aphelocoma californica immanis, Oberholser (1917:95, not of Grinnell, 1901), part; Swarth (1918:415, not of Grinnell or Oberholser), part.

Aphelocoma californica superciliosa, van Rossem (1933:346), part.

Aphelocoma coerulescens immanis, Hellmayr (1934:51), part.

Aphelocoma coerulescens superciliosa, A.O.U. Check-list Committee (1945:445), part.

Type.—No. 1431a, Strickland Collection, University of Cambridge; collected in "California" (Strickland, 1845a:260; van Rossem, 1933:345); exact locality and collector unknown; first-year bird, probably a female, in fresh fall plumage. Van Rossem's measurements (letter) are as follows (mm.): wing, 115; tail, 128; tarsus, 40.2.

Nomenclatural history.—A larger, interior form of the Pacific coast scrub jay was first separated from *A. californica* by Grinnell in 1901 under the name *immanis*, but it was denied recognition by the A.O.U. nomenclatural committee until 1918. Grinnell initially defined *immanis* on the basis of specimens from the Willamette Valley of Oregon, but in 1917 Oberholser extended the range of *immanis* into north-central California and in 1918 Swarth concluded that jays from all interior California north of Mount Pinos were of that race.

An earlier name, *superciliosa* of Strickland (1845a), was later found for Swarth's race *immanis*. Van Rossem (1933) examined Strickland's type of *Cyanocitta superciliosa* and found it to be comparable to specimens from the Sacramento Valley. He suggests (*ibid.*:346) that the type was probably obtained by one of the early Russian expeditions which penetrated the interior from San Francisco, since the type was obtained by Strickland from J. F. Brandt of St. Petersburg (van Rossem, letter). Since the type was not identified as either a first-year or an adult specimen by van Rossem in his published discussion of it, the possibility remained that it might be a first-year bird of one of the coastal races, thus paler than corresponding adults and only suggestive of the valley race. However, van Rossem (letter) describes the type as "a bird of the year with . . . narrow and more pointed rectrices"; little doubt remains, then, as to his appraisal of the color characters.

The Sacramento Valley was suggested by van Rossem (1933:346) as a type locality; but, as can now be understood from the previous discussions of variation (p. 256), it matters little in what part of the Sacramento Valley the type locality falls: the scrub jays of that part of California are exceptionally variable and too weakly differentiated, considered separately from other interior areas, to be separated satisfactorily from coastal races on a nomenclatural basis. Sacramento, in Sacramento County, as a probable site visited by early Russian explorers, is here suggested as the restricted type locality.

My examination of the entire complex of scrub jays occupying interior California and Oregon has led to the recognition of two separate races and the employment of both the names *immanis* and *superciliosa*. As shown above, characters ascribed here to the race *superciliosa* are seen most strongly developed in specimens from northeastern California and Washoe County, Nevada. Little material from these areas has been available to previous students of this species, and the extreme development there of certain trends suggested by specimens from the San Joaquin Valley has not been fully described heretofore. Thus there is adequate basis for the early suggestions of Henshaw (1877:1305), who stated that "California jays

... of the eastern slope not only have smaller bills and feet than coast examples, but their colors throughout are decidedly lighter," and Ridgway (1877b:525), who noted that specimens from the Carson City area have pale gray backs and pure white under parts. These observations contrast obviously with Grinnell's (1901:188) original characterization of *immanis*, *sensu stricto*: "In coloration similar to *Aphelocoma californica*, but size greater."

Specimens examined.—Total, 640, divided as follows: (1) Sacramento Valley, south to Contra Costa, San Joaquin, and Tuolumne counties, 238 (tables 17 and 18); (2) San Joaquin Valley and the southern Sierra Nevada, 172 (table 19); (3) eastern slopes of the Sierra Nevada, Inyo County, 49 (table 20); (4) north-central California (Shasta and Siskiyou counties) and south-central Oregon (Jackson and Klamath counties), 43 (table 21); (5) south-central Oregon (Lake County), northeastern California, and northwestern Nevada, 138 (table 22).

1) *Tehama County*: Anderson, 1; Battle Creek, 1; mouth of Battle Creek, 3; 2 mi. E Beegum, 4; 2 mi. SE Beegum (1,650 ft.), 4; Inskip Hill, 2; Manton, 3; Paine Creek, 2; Red Bluff, 7. *Plumas County*: Quincy, 1. *Glenn County*: 5 mi. W Fruto, 4. *Butte County*: 10 mi. S, 6 mi. W Chico, 2; 7 mi. W Chico, 1; Gridley, 1; Jonesville, 1; 4 mi. N Oroville, 1; Paradise, 1. *Yuba County*: Marysville, 1; Rackerby, 21. *Sutter County*: Marysville Buttes, 2; West Butte, 2. *Colusa County*: Fouts Springs (base of Snow Mountain), 2; 5 mi. W Maxwell, 1; 7 mi. W Sites, 1; Stonyford, 6. *Nevada County*: Grass Valley, 2. *Placer County*: Applegate, 19; Cisco (6,000 ft.), 1; Clipper Gap, 3; Colfax, 1; Rocklin, 4. *Eldorado County*: Cool, 2; 4 mi. W Placerville, 1. *Amador County*: 5 mi. E Carbondale, 2; Carbondale, 4; Drytown, 1; Jackson, 4. *Calaveras County*: Angels Camp, 8; San Andreas, 78. *Tuolumne County*: unspecified, 1. *Sacramento County*: Courtland, 1; 7½ mi. N Courtland, 1; Hyde, 1; Snodgrass Slough, 1; unspecified, 3. *Yolo County*: Davis, 3; Grafton, 2; Grand Island, 3. *Solano County*: 3 mi. W Vacaville, 5. *Contra Costa County*: Mount Diablo, 6; Nortonville (600 ft.), 5; Somersville, 1.

2) *San Joaquin County*: Linden, 1; Lodi, 1; Tracy, 3. *Stanislaus County*: La Grange, 1; Modesto, 3; 2 mi. S Orestimba Peak, 12; Patterson, 1. *Merced County*: 10 mi. E Los Banos, 1; Planada, 2; Snelling, 4. *Mariposa County*: 3 mi. NE Coulterville, 1; Dudley, 1; El Portal, 7; Mariposa, 6; Smith Creek (2,900 ft.), 1. *Madera County*: Raymond, 1; San Joaquin Experimental Range, 2. *Fresno County*: 7 mi. E Dos Palos (185 ft.), 1; Dunlap, 4; 3½ mi. E Dunlap, 2; 3 mi. W Miramonte, 1; Minkler, 14; Shaver, 4. *Tulare County*: Kern River (25 mi. N Kernville), 1; 2 mi. W Lindsay, 3; Porterville, 10; Golden Trout Creek (6,000–7,000 ft.), 7. *Kern County*: Bodfish, 1; 12 mi. N Caliente, 1; Cannell Meadow, 2; Fort Tejon, 1; Kelso Valley, 6; 8 mi. W, 3 mi. N McKittrick (2,100 ft.), 24; 10 mi. NW McKittrick, 4; 14 mi. N, 6 mi. W McKittrick (3,500 ft.), 2; Mount Pinos, 2; Onyx, 1; Piute Mountains, 4; Tehachapi, 3; 2 mi. W Temblor Ranch (3,100–3,200 ft.), 4; Walker Basin: SW Point (3,350 ft.), 1, Rankin Ranch, 2, and Thompson Canyon, 8; Walker Pass, 3; 6 mi. N Weldon, 5. *Ventura County*: Mount Pinos, 3.

3) *Inyo County*: Carroll Creek (5,500 ft.), 1; 5 mi. W, 1¼ mi. S Independence (Little Pine Creek, 6,000 ft.), 12; 5 mi. W, 3 mi. S Independence (Pinyon Creek, 6,500 ft.), 4; 4 mi. W, ½ mi. N Independence (5,200 ft.), 5; Keamsarge Pass (6,000–7,000 ft.), 2; 6 mi. W, 2 mi. S Lone Pine (6,300–6,600 ft.), 6; 4 mi. SW Olancha (Walker Creek, 5,200–7,500 ft.), 18; Round Valley (approx. 12 mi. S Mount Whitney), 1.

4) CALIFORNIA. *Shasta County*: Baird, 2; Dana, 1; 1 mi. N Subway Cave (3,400 ft.), 1. *Siskiyou County*: Bogus, 1; Gazelle Mountain (= Antelope Mountain, near Gazelle?), 5; Hornbrook, 2; Picard, 1; Sisson, 3; 11 mi. NE Weed, 2; Yreka, 2.

OREGON. *Jackson County*: Brownsboro, 2; Colectin, 3; Eagle Point, 10; Medford, 3; Siskiyou, 1. *Klamath County*: 8 mi. W Bly, 1; 8 mi. E Klamath Falls, 2; Klamath Falls, 1.

5) OREGON. *Lake County*: Adel, 3; 9 mi. S Adel, 10; 10 mi. N Adel, 1; 6 mi. W Adel, 1; 14 mi. SW Adel, 1; Hart Mountain, 1; Lakeview, 2; 15 mi. E Lakeview, 1; 5 mi. NE Lakeview, 2; Summer Lake, 8; S Warner Valley, 3; Warner Mountains, 2.

CALIFORNIA. *Modoc County*: Alturas, 1; 17 mi. NNW Alturas, 1; 32 mi. NNW Alturas, 1; 10 mi. SW Alturas, 2; Cedarville, 2; 5 mi. S Cedarville, 1; Eagleville, 7; Fandango Mountain, 3; Juniper Butte, 1; Lake City, 1; Warner Mountains: Dry Creek (4,750–5,000 ft.), 14, Parker

Creek, 8, Sugar Hill, 2, and Shields Creek, 1. *Lassen County*: 6 mi. NW Amadee, 1; 15 mi. S Doyle, 2; 5 mi. W Fredonyer Peak, 2; Grasshopper Valley, 1; Jones, 2; 4 mi. SW McDonald Peak, 3; 3 mi. W Observation Peak, 1; 6 mi. N Observation Peak, 2; 8 mi. SW Ravendale, 3; 8 mi. NE Susanville, 1; Termo, 1. *Sterra County*: Little Truckee River (N of Independence Lake), 1. *Nevada County*: Independence Lake, 1. *Placer County*: $\frac{1}{2}$ mi. N Ward Creek (Lake Tahoe), 1. *Eldorado County*: Bijou (Lake Tahoe), 1; Rowland Marsh (Lake Tahoe), 1. *Alpine County*: Fredericksburg, 1; 3 mi. E Woodfords, 3.

NEVADA. *Ormsby County*: Carson City, 3. *Washoe County*: Franktown, 1; E base Granite Mountain, 1; Peavine Mountain (NW Reno), 1; 17 mi. NW Reno (6,000 ft.), 2; $2\frac{1}{2}$ mi. W Reno Hot Springs, 1; Twelve-mile Creek ($\frac{1}{2}$ mi. E state line, 5,300 ft.), 9; 2 mi. E, 1 mi. S Steamboat Springs, 5; Virginia Mountains ($2\frac{1}{2}$ mi. W Sutcliffe), 5; S end Washoe Valley (4,700 ft.), 1. *Douglas County*: Gardnerville, 1.

***Aphelocoma coerulescens immanis* Grinnell**

Corvus ultramarinus, Audubon (1838:456), part.

Garrulus ultramarinus, Audubon (1839:154), part.

Cyanocitta californica, Baird (1858:xli), part.

Cyanocitta floridanus californicus, Henshaw (1879:307), part.

Aphelocoma californica, Anthony (1886:167), part.

Aphelocoma californica immanis Grinnell (1901:188), original description; Oberholser (1917:95, not of Grinnell), part; Swarth (1918:415, not of Grinnell or Oberholser), part.

Aphelocoma californica californica, Ridgway (1904:327), part.

Aphelocoma californica superciliosa, van Rossem (1933:346), part.

Aphelocoma coerulescens immanis, Hellmayr (1934:51), part.

Aphelocoma coerulescens superciliosa, A.O.U. Check-list Committee (1945:445), part.

Type.—Adult male, no. 33789, MVZ; Scio, Linn County, Oregon; collected by A. G. Prill, January 9, 1901 (no original collector's number); orig. no. 4582, collection of Joseph Grinnell. Plumage slightly worn; breast lightly stained. Measurements (mm.): wing, 131.2; tail, 146.9; bill length, 20.5; bill depth, 9.6; bill width, 9.3; tarsus, 43.5.

Nomenclatural history.—*Immanis*, as a large race of the scrub jay, was described by Grinnell in 1901 from specimens taken in the Willamette Valley. Its range was later extended southward into interior California. Other developments in the use of the name *immanis* have been discussed (p. 396). *Immanis*, as recognized here, is restricted to the Willamette Valley; the use of the name is thus identical with that originally proposed by Grinnell.

Specimens examined.—Total, 45 (table 23). WASHINGTON. *Clark County*: Ridgefield, 3; Vancouver, 2.

OREGON. *Multnomah County*: Portland, 1; 5 mi. E Portland, 1; Sauvie Island, 7. *Washington County*: Beaverton, 2; Forest Grove, 4. *Tillamook County*: 9 mi. SE Tillamook, 1. *Marion County*: Salem, 11. *Linn County*: Albany, 3; Scio, 9. *Wasco County*: "Columbia River" [= The Dalles], 1.

***Aphelocoma coerulescens insularis* Henshaw**

Cyanocitta floridana, var. *californica*, Henshaw (1876:253), part.

Aphelocoma insularis Henshaw (1886:452), original description.

Aphelocoma coerulescens insularis, Hellmayr (1934:53).

Cyanocitta coerulescens insularis, Amadon (1944a:4).

Type.—Described by Grinnell (1932:288) as follows: "[male?] adult; skin in good condition; collected by Henry W. Henshaw, June 2, 1875; orig. no. 733; now

no. 79695, U. S. Nat. Mus. . . . *Type locality*, Santa Cruz Island, Santa Barbara County," California. My measurements of the type are as follows (mm.): wing, 132.4; tail, 147.6; bill length, 21.2; bill depth, 10.8; bill width, 9.0; tarsus, 43.0; hind toe, 14.2; middle toe, 21.1. These data indicate that the type is probably a female.

Nomenclatural history.—See the synonymy given above. The proposal of Hellmayr (1934:53) that *insularis*, long accorded specific rank, be regarded as a race has been accepted by the A.O.U. Check-list Committee (1944:453).

Specimens examined.—Total, 279 (table 24). *Santa Barbara County*: Santa Cruz Island, 279 (including type).

***Aphelocoma coerulescens woodhouseii* (Baird)**

Cyanocorax ultramarinus (not *Corvus ultramarinus* Bonaparte), McCall (1851:216), part.

Cyanocitta woodhouseii Baird (1858:585), original description, part.

Cyanocitta californica (not of Strickland), Henry (1860:108), part.

[*Cyanurus*] *woodhouseii*, Gray (1870:4), part.

Cyanocitta floridana, Allen (1871:298), part.

Aphelocoma floridana var. *woodhousei*, Allen (1872:150), part.

Cyanocitta californica var. *woodhousei*, Ridgway (1873a:169), part.

Cyanocitta floridana var. *woodhousei*, Ridgway (1873a:169), part.

[*Aphelocoma floridana* var. *woodhousei*] *b. woodhousei*, Coues (1874b:219, in synonymy), part.

Aphelocoma woodhouseii, Ridgway (1877a:208), part.

Aphelocoma cyanotis, Fisher (1894:327), part.

Aphelocoma texana, Ridgway (1902:70), part.

Aphelocoma californica woodhouseii, Oberholser, 1917:95), part.

Aphelocoma coerulescens woodhouseii, Hellmayr (1934:53), part; Pitelka (1945a:24, not of Hellmayr).

Aphelocoma coerulescens texana, Hellmayr (1934:54), part.

Type.—Adult specimen of unknown sex, no. 8484, USNM; Fort Thorn, ten miles west of Rincon, 4,500 feet, Doña Ana County, New Mexico; collected by T. C. Henry (Bailey, 1928:12, 48). My measurements of the type are as follows (mm.): wing, 135.1; tail, 142.1; bill length, 19.1; bill depth, 8.8; bill width, 8.0; tarsus, 41.2; hind toe, 12.5; middle toe, 18.6. The plumage of the type is moderately worn, and it was probably collected in the spring. The crown is both soiled and worn; it is thus darker and more purplish than in fresh-plumaged specimens. The under tail coverts are tipped with dull blue; the belly is whitish.

Nomenclatural history.—Treated together with that of *nevadae*; see p. 400.

Specimens examined.—Total, 263, divided as follows: (1) eastern Utah, Colorado, northeastern Arizona, northern New Mexico, extreme western Oklahoma, and southwestern corner of Kansas, 179 (table 26); (2) southern New Mexico and western Texas, 84 (table 27).

1) COLORADO. *Archuleta County*: Arboles, 1; Pagosa Junction, 1. *Bent County*: Fort Lyon, 2. *Boulder County*: unspecified (5,500 ft.), 1. *Chaffee County*: Buena Vista, 1; Salida, 1. *Delta County*: Paonia, 1. *Denver County*: Denver, 6. *Douglas County*: Castle Rock, 1; Sedalia, 4; unspecified, 1. *El Paso County*: Colorado City, 2; Colorado Springs, 11. *Garfield County*: Glenwood Springs, 1; Meeker (near Rifle), 1; Newcastle, 35; unspecified, 2. *Jefferson County*: Platt Canyon, 1; Turkey Creek, 1. *La Plata County*: Animas River, 1; Bondad, 3; Durango, 1. *Las Animas County*: unspecified, 1. *Montrose County*: Montrose, 1; Paradox, 1; Paradox Valley, 4. *Montezuma County*: Ackman, 1; Paiute Peak, 4. *Pueblo County*: Beulah, 2; Pueblo, 1; unspecified, 7. *Rio Blanco County*: Rangely, 1.

UTAH. *Garfield County*: Henry Mountains, 1. *Grand County*: Cisco, 1; La Sal Mountains (15

mi. SE Moab, 6,000 ft.), 1; Moab, 2; 20 mi. N Moab (on Colorado R.), 1. *Kane County*: Kaiparowits Plateau, 3. *Salt Lake County*: Emigration Canyon (5,500 ft.), 1; 5 mi. SE Union, 1. *San Juan County*: Bluff, 1; 19 mi. SE Moab (Block Canyon, 5,400 ft.), 2; Goulding, 1; Navajo Mountain, 2. *Sanpete County*: 2 mi. N Fairview (6,100 ft.), 1. *Sevier County*: Fish Lake, 2. *Utah County*: Hill Creek, 40 mi. S Ouray, 1; 10 mi. NW Vernal, 1; 20 mi. N Vernal, 1; 25 mi. E Vernal (Blue Mountain, 8,000 ft.), 1. *Utah County*: Provo, 2. *Weber County*: Ogden, 1; 2 mi. NE Ogden (4,500 ft.), 6; 3 mi. NE Ogden (5,500 ft.), 1.

ARIZONA. *Cocconino County*: 5 mi. S Navajo Mountain, 1. *Navajo County*: 19 mi. SW Kayenta, 1; 2 mi. SE Burnheimer Bridge (4,800 ft.), 1.

NEW MEXICO. *Colfax County*: Cimarron, 1; Preston, 1. *McKinley County*: Gallup, 1. *San Juan County*: Aztec, 1; Fruitland, 1. *San Miguel County*: Las Vegas, 6. *Santa Fe County*: San Pedro, 1. *Taos County*: 2 mi. N Arroyo Seco (8,000 ft.), 1; Burgwin, 1; Rinconada (5,600 ft.), 1; Taos (7,000–7,500 ft.), 5. *Union County*: Folsom, 4. *Valencia County*: Rio Puerco, 1.

KANSAS. *Morton County*: 12 mi. NE Elkhart, 4.

OKLAHOMA. *Cimarron County*: Kenton, 11.

2) NEW MEXICO. *Catron County*: Glenwood (5,000 ft.), 1; Reserve, 6. *Doña Ana County*: Doña Ana (3,800 ft.), 2; Fort Thorn, 1 (type); Las Cruces, 4; 5 mi. W Las Cruces (3,800 ft.), 1; Organ Mountains (6,000–6,700 ft.), 2. *Eddy County*: Queen (6,500 ft.), 2. *Grant County*: Gila, 1; Rio Mimbres, 1. *Lincoln County*: Alto (8,000 ft.), 1; Ancho, 3; Corona, 1; Jicarilla, 2; Sierra Capitan, 2. *Luna County*: Deming, 1; Florida Mountains, 1. *Otero County*: Mescalero, 2. *Sierra County*: unspecified, 1. *Torrance County*: Manzano Mountains, 1.

TEXAS. *Brewster County*: Alpine, 1; 4 mi. W Alpine, 4; 5 mi. S Alpine, 1; 10 mi. W Alpine (Paisano Pass, Paisano Peak), 2; Glass Mountains (15 mi. NE Marathon), 1; 12 mi. N Marathon, 2; 20 mi. SW Marathon, 1; Paisano, 7. *Culberson County*: Frijole (5,900–8,500 ft.), 6. *El Paso County*: Ysleta, 1. *Jeff Davis County*: Davis Mountains, 6; 4 mi. N Fort Davis, 2; 5 mi. E Livermore (5,400–5,500 ft.), 11; Mount Locke (5,500–6,100 ft.), 2. *Armstrong County*: 15 mi. SW Claude, 1.

***Aphelocoma coerulescens nevadae* Pitelka**

Cyanocorax californica, Woodhouse (1853:77), part.

Cyanocitta californica, Kennerly (1856:16), part.

Cyanocitta woodhouseii, Baird (1858:585), part.

[*Cyanurus*] *woodhouseii*, Gray (1870:4), part.

Cyanocitta floridana, Allen (1871:298), part.

[*Aphelocoma floridana*] var. *woodhousei*, Coues (1872:166), part.

Cyanocitta floridana var. *woodhousei*, Henshaw (1874:123), part.

[*Aphelocoma floridana* var. *woodhousei*] b. *woodhousei*, Coues (1874b:219, in synonymy), part.

Cyanocitta californica var. *woodhousei*, Baird, Brewer, and Ridgway (1874:291), part.

Aphelocoma woodhousei, Sharpe (1877:114), part.

Cyanocitta var. *woodhousei*, Henshaw (1877:1310), part.

Aphelocoma californica woodhousei, Oberholser (1917:95), part.

Aphelocoma coerulescens woodhousei, Hellmayr (1934:53), part.

Aphelocoma coerulescens nevadae Pitelka (1945a:24), original description.

Aphelocoma californica nevadae, A. H. Miller (1946:58).

Type.—Adult male, no. 28080, MVZ; three miles east of Jackass Springs, 6,200 feet, Panamint Mountains, Inyo County, California; collected by Joseph Grinnell, September 30, 1917; orig. no. 4509.

Nomenclatural history.—From the time the scrub jay of the Rocky Mountains region was first recognized as distinct from Californian, Floridan, and Mexican forms of *Aphelocoma* under the name *woodhousei* (Baird, 1858:585), only minor changes have occurred in its geographic and nomenclatural delimitation. Near the turn of the century, scrub jays of western Texas were considered to represent *cyanotis* (Fisher, 1894:327) and *texana* (Ridgway, 1902:70), but some years

later Oberholser (1917:94) showed that the area in question was one of intergradation between *woodhouseii* and *texana*. Later authors (e.g., Van Tyne and Sutton, 1937:59) have identified jays of western Texas as *woodhouseii*.

Oberholser (1917:94) also held that *woodhouseii*, regarded as a species over the preceding forty years, represented one of a series of races including those of the California mainland, Oregon, and Mexico, linked together by direct intergradation or by overlap in individual variation of the widely separated races *sumichrasti*, *hypoleuca*, and *immanis* (= *superciliosa*). Both Oberholser (1918:166, 167), his earlier action notwithstanding, and Swarth (1918:406) agreed in considering *woodhouseii* as specifically distinct from the "*californica*" complex in the absence of evidence that "*woodhouseii*" of Nevada (= *nevadae*) and "*immanis*" (= *superciliosa*) interbreed directly; but Swarth argued that the two could not be regarded as conspecific on the basis of overlap in individual variation as did Oberholser earlier. Swarth apparently overlooked the need for the use of a trinomial when he set *woodhouseii* apart from *californica*, since *woodhouseii* was then known to intergrade with *texana* and probably with other races to the south (Oberholser, 1917:94).

After twenty years or so, Linsdale (1938:36), reporting on newly acquired specimens from Nevada, maintained that comparisons of measurements of "*immanis*" and "*woodhouseii*" "show small average differences of about the same magnitude and paralleling in direction those found in other variable species of the same region" and that certain specimens were intermediate in color. For these reasons Linsdale concluded that the two forms were conspecific, but he offered no proof of actual interbreeding. Results of my studies of the relationships of *superciliosa* and *nevadae* (discussed in full on p. 295) are not in agreement with those of Linsdale. For the most part, previous discussions of relationships and nomenclature of "*woodhouseii*" and "*immanis*," those cited above as well as others, have not been supported by any conclusive evidence.

Specimens examined.—Total, 388, divided as follows: (1) Nevada, southwestern Oregon, southern Idaho, and western Utah, 66 (table 30); (2) Mono, Inyo, and San Bernardino counties of southeastern California and bordering parts of Nevada, 129 (table 29); (3) Arizona, extreme south-central Utah, and extreme southwestern New Mexico, 193 (table 31).

1) NEVADA. *Churchill County*: 4 mi. W Fallon (4,000 ft.), 1. *Clark County*: ½ mi. N California-Nevada Monument, Colorado River (500 ft.), 1; Kaolin, 2; Sheep Range (8,500 ft.), 1; Virgin Mountains (Cedar Basin), 1. *Elko County*: W side Ruby Valley (3 mi. N Elko County line), 6. *Eureka County*: Eureka, 1. *Humboldt County*: Quinn River Crossing, 1. *Lander County*: Kingston Creek (6,900 ft.), 4; mouth of Kingston Canyon (6,000 ft.), 1. *Lincoln County*: Mount Irish (Springer Spring, 7,000 ft.), 3. *Nye County*: 4 mi. N Hot Creek (6,500 ft.), 1; Monitor Range, 1; Greenmonster Canyon (7,500 ft., Monitor Range), 2; Quinn Canyon Mountains: Burned Corral Canyon (7,600 ft.), 1, and 7 mi. E Nyala (7,000 ft.), 1; Round Mountain (6,000 ft.), 1; Toiyabe Mountains: Ophir Creek (8,000 ft.), 2, South Twin River (6,700 ft.), 2, and Wisconsin Creek (7,000–7,800 ft.), 2. *Washoe County*: Sutcliffe, 1; Granite Creek, 1. *White Pine County*: Snake Mountains: Hendry Creek (6,800 ft.), 1, and Lehman Creek (7,000–7,500 ft.), 4; W side Ruby Lake (3 mi. S White Pine County line, 6,100 ft.), 1; Willow Creek (2 mi. S White Pine County line, Ruby Mountains), 1; E side Schellbourne Pass (6,800 ft.), 1.

UTAH. *Beaver County*: Minersville, 1. *Bow Elder County*: Kelton, 1. *Iron County*: Cedar City, 2. *Millard County*: Cove Fort, 1. *Washington County*: Bellevue (4,500 ft.), 2; 5 mi. NW Leeds (4,200 ft.), 3; Jackson's Spring, 1; Pine Valley, 1; 4 mi. E Pine Valley (7,000 ft.), 1; 2 mi. N Pinto, 2; 2 mi. SE Pinto (6,500 ft.), 3.

OREGON. *Harney County*: Andrews, 1; 4 mi. N Andrews, 1.

IDAHO. *Cassia County*: Bridge, 1.

2) CALIFORNIA. *Mono County*: 5 mi. W, 4 mi. N Benton (6,800–7,000 ft.), 9; 8 mi. W, 1½ mi. N Benton (7,600 ft.), 3; 4 mi. W Benton (Dutch Pete's Ranch, 6,482 ft.), 1; 5 mi. N Benton (Pellissier Ranch, 5,600 ft.), 1; 1½ mi. N, 3 mi. E Benton Station (6,900–9,000 ft.), 7; 2 mi. S Benton Station (Taylor's Ranch, 5,300 ft.), 1; White Mountains (McCloud Camp, 9,200 ft.), 2; Williams Butte (7,000 ft.), 2. *Inyo County*: Argus Range (Mountain Spring Canyon, 6,600 ft.), 3; E side Deep Springs Lake (5,000 ft.), 1; Haskett Trail (S of Carroll Creek, 8,500 ft.), 1; Keeler (3,600 ft.), 1; NE of Lone Pine (3,750 ft.), 2; 6 mi. W, 1 mi. S Lone Pine (6,600 ft.), 1; 6 mi. N Lone Pine, 1; Panamint Mountains: Panauyah Canyon (7,500 ft.), 3; Johnson Canyon (6,000 ft.), 6; 3 mi. E Jackass Springs (6,200 ft.), 9 (including type); and unspecified (8,000 ft.), 1; E base Waucoba Mountain (7,300 ft.), 5; White Mountains: Cedar Flat, 2, 2 mi. NW Roberts Ranch (9,000 ft.), 1, Silver Canyon (7,000–8,000 ft.), 6, Westgaard Pass (7,300 ft.), 2, Wyman Creek (7,500–8,000 ft.), 5, and unspecified, 1. *San Bernardino County*: SE side Clark Mountain (5,000–7,000 ft.), 8; Colorado R. (29 mi. S Needles, 420 ft.), 2; Kingston Range (Horse Springs, 4,750–5,500 ft.), 3; Providence Mountains: Cedar Canyon (5,000 ft.), 5, and 5 mi. N Granite Wells (5,400 ft.), 3.

NEVADA. *Clark County*: Charleston Mountains (6,000–6,200 ft.), 4; N side Potosi Mountain (5,800–7,500 ft.), 4. *Douglas County*: 9 mi. SSE Gardnerville (5,500 ft.), 2; 10 mi. SE Gardnerville, 1; 1 mi. NNW Holbrook (5,800 ft.), 1. *Esmeralda County*: 3 mi. S Cave Spring (7,500 ft.), 1; Silver Peak, 2; White Mountains (Chiatovich Creek, 8,000 ft.), 1; Mount Magruder (6,400–7,700 ft.), 8. *Mineral County*: Excelsior Mountains (Endowment Mine, 6,500 ft.), 1; 2 mi. SW Pine Grove (7,250 ft.), 1. *Nye County*: 5 mi. E, 1 mi. S Grapevine Peak (6,000 ft.), 1; 3 mi. E Grapevine Peak (6,000–6,700 ft.), 4.

3) ARIZONA. *Apache County*: Springerville, 1; 4 mi. S Springerville, 2. *Cochise County*: Apache, 1; Bisbee, 1; Chiricahua Mountains, 39; Dragoon Mountains, 5; Galeyville (Turkey Creek Canyon), 1; Huachuca Mountains, 20; Paradise, 16; Rincon Mountains, 1; Whetstone Mountains, 5; unspecified, 1. *Cocconino County*: Deadman's Flat (6,400 ft., NE of San Francisco Mountain), 2; San Francisco Mountain, 1. *Gila County*: Indian Gardens, 1; Payson, 4; Roosevelt, 1. *Greenlee County*: Blue River, 1. *Maricopa County*: Phoenix, 4; Tempe, 1. *Mohave County*: Chemehuevi Mountain (6,400 ft.), 2; Moecasin, 1; Mount Trumbull, 1. *Navajo County*: Fort Apache, 1; Keam Canyon, 1; 8 mi. S Whiteriver, 9. *Pima County*: Rosemont, 2; Santa Catalina Mountains (3,000–3,500 ft.), 5; Santa Rita Mountains, 1; Tucson (including Fort Lowell), 7. *Pinal County*: Catalina Mills, 7; Oracle, 4. *Yavapai County*: Agua Fria (between Prescott and Fort Verde), 1; Cherry Creek, 1; Fort Verde, 3; Mayer, 6; Prescott, 18. (For localities see Barnes, 1935.)

UTAH. *Kane County*: 10 mi. N Kanab (5,500 ft.), 1; 5 mi. N Kanab (5,300 ft.), 1; 5 mi. NW Kanab (5,500 ft.), 8; 3½ mi. NW Kanab (5,600 ft.), 1.

NEW MEXICO. *Catron County*: Cactus Flat (40 mi. NW Silver City), 1. *Grant County*: Sierra Hachita, 1. *Hidalgo County*: San Luis Mountains, 1.

SONORA: San José Mountains, 1.

Aphelocoma coerulescens texana Ridgway

Aphelocoma woodhousei (not *Cyanocitta woodhouseii* Baird), Lloyd (1887:290).

Aphelocoma cyanotis, Bendire (1895:382), part.

Aphelocoma texana Ridgway (1902:70), original description, part.

Aphelocoma californica texana, Oberholser (1917:95).

Aphelocoma coerulescens texana, Hellmayr (1934:54), part.

Type.—Adult female, no. 150507, USNM; near head of Nueces River, Edwards County, Texas; taken by H. P. Attwater, December 1, 1894 (Ridgway, 1903:70; but see Lacey, 1903:151, who apparently collected the type and sent it to Attwater). My measurements of the type are as follows (mm.): wing, 127.1; tail, 123.8; bill length, 17.6; bill depth, 9.3; tarsus, 40.0.

Nomenclatural history.—Before the scrub jays of west-central Texas were recognized by Ridgway (1902) as a distinct race, they had been called both *woodhouseii* and *cyanotis*, which occur to the west and south, respectively. *Cyanotis* was first reported from Texas by Fisher in 1894 on the basis of three specimens taken at Paisano, Brewster County. Shortly thereafter, the range of this race in the United States was extended east to Edwards and Kerr counties (Bendire, 1895:382). After separating the scrub jays of west-central Texas under the name *texana*, Ridgway (1904:335) continued to ascribe *cyanotis* to Texas, limiting its range to a belt from the southern portion of the trans-Pecos region east to Sutton and Kerr counties. The range of *cyanotis* was thus confused with that of *texana*, described from a specimen taken in Edwards County and said by Ridgway (1904:337) to extend from the Davis Mountains to Concho and Kerr counties. Very little fresh-plumaged material was available to him and other earlier students, however. In 1917, on the basis of a good series of fresh-plumaged specimens, Oberholser was able to show that *cyanotis* did not occur north of the Mexican boundary and that the scrub jays of west-central Texas were all of the race *texana*.

With respect to the past application of the names *texana* and *woodhouseii* to the scrub jays of the trans-Pecos region, both were used by Ridgway (1904:333, 337), who considered the Davis Mountains as the meeting ground of the two races. Oberholser (1917:94), after eliminating the name *cyanotis*, said only that intergradation between *texana* and *woodhouseii* occurred in the Davis Mountains. In the same year Smith (1917:163) reported that all specimens which he collected in the Davis Mountains appeared to be *woodhouseii*. Although Oberholser (1920:91) later stated that the range of *texana* included the Davis, Chinati, and Chisos mountains, more recently he has found that scrub jays of that region show some trends toward *texana*, but are best regarded as *woodhouseii* (see Van Tyne and Sutton, 1937:59). Results of my studies support this more recent opinion. Hellmayr's (1934:54) ascription of *texana* to Jeff Davis and Brewster counties is based on three specimens in the Field Museum collection which show a marked approach toward *texana*; elsewhere I have shown that the preponderance of specimens from this region represent *woodhouseii*.

Specimens examined.—Total, 123 (table 32). TEXAS. *Crockett County*: 15 mi. E Sheffield, 1. *Edwards County*: head of Nueces River, 1 (type); 7 mi. S Rocksprings, 2; unspecified, 2. *Kerr County*: Ingram, 19; Kerrville, 65; Japonica, 2; 15 mi. W Japonica, 2; 20 mi. W Mountain Home, 2; unspecified, 4. *Kimble County*: Junction, 5. *Sutton County*: Sonora, 2; unspecified, 16.

Aphelocoma coerulescens grisea Nelson

A[phelocoma] woodhousei, Ridgway (1887:355), part.
Aphelocoma grisea Nelson (1899b:27), original description.
Aphelocoma cyanotis, A.O.U. Check-list Committee (1902:321), part.
Aphelocoma californica grisea, Oberholser (1917:95).
Aphelocoma coerulescens grisea, Hellmayr (1934:54).

Type.—Adult female, no. 164250, BS; near Guachochic (26°45' N, 107°01' W), north of Río Fuerte, Sierra Madre, southern Chihuahua; taken by E. A. Goldman, September 27, 1898 (Nelson, 1899b:27).¹⁴ My measurements of the type are as

¹⁴ I am indebted to R. T. Moore for corroborative information on this type locality.

follows (mm.) : wing, 132.9; tail, 137.2; bill length, 17.2; bill depth, 7.9; tarsus, 37.5.

Nomenclatural history.—Since it was first described by Nelson, the race *grisea*, per se, has received attention only from W. DeW. Miller (1906). All later changes in its nomenclature are based on synoptic studies of the specific status of *californica* or *coerulescens* and closely allied races. *Grisea* remains one of the poorly understood races of the scrub jay.

Specimens examined.—Total, 20 (table 33). CHIHUAHUA: Bustillos, 5; near Guachochic, 1 (type). DURANGO: Cerro Prieto, 1; La Boquilla (7,000 ft.), 2; Las Bocas, on Río de Florita (6,800 ft.), 4; Rosario (7,500 ft.), 5; Santuario (7,000 ft.), 2.

Aphelocoma coerulescens cyanotis Ridgway

Cyanocitta woodhouseii, Baird (1858:585), part.

Cyanocitta californica, Sclater and Salvin (1869:362), part.

[*Cyanocitta californica*] var. *sumichrasti*, Baird, Brewer, and Ridgway (1874:283), part.

Aphelocoma sumichrasti, Stone (1890:214), part.

A[phelocoma] cyanotis Ridgway (1887:357), original description; Ridgway (1896:613), part; A.O.U. Check-list Committee (1902:321, not of Ridgway), part; Miller (1906:170, not of A.O.U. Check-list Committee).

Aphelocoma californica cyanotis, Oberholser (1917:95).

Aphelocoma coerulescens cyanotis, Hellmayr (1934:55).

Type.—Adult specimen of unknown sex, no. 8465, USNM; Mexico; collected by John Taylor, September, 1836 (Ridgway, 1887:357); obtained from John Gould (Baird, 1858:586). This specimen is one of a series presented to the British Museum in 1841 by Taylor, who obtained them from Morgan of Real del Monte, Hidalgo (Sharpe, 1906:497). The latter locality may therefore be considered the restricted type locality (H. G. Deignan, MS). My measurements of the type are as follows (mm.) : wing, 134.2; tail, 133.2; bill length, 16.5; bill depth, 8.8; tarsus, 39.4; hind toe, 12.0; middle toe, 18.1. The specimen is soiled but in fresh plumage. Coloration is dull; this fact together with the measurements given here indicate that the type is probably a female.

Nomenclatural history.—At the turn of the century, the race *cyanotis*, then treated as a species, was thought to have a wide distribution, ranging into areas occupied by *texana*, *woodhouseii*, and *grisea*. The details of this situation have been presented elsewhere (pp. 305, 403).

Specimens examined.—Total, 81, divided as follows: (1) San Luis Potosí, México, Federal District, and Hidalgo, 67 (table 34); (2) southeastern Coahuila, 14 (table 35).

1) SAN LUIS POTOSÍ: Bocas, 5; 25 mi. W Charcas (7,000–8,000 ft.), 4; Jesús María, 6; La Parada, 2; Morales, 3; Río Verde, 3; San Luis Potosí, 7; Saucito, 7; Villa de Reyes, 1; Ypiña, 22. MÉXICO: Progreso (19°37' N, 99°23' W), 1. FEDERAL DISTRICT: Mexico City, 1; Santa Rosa (2,900 m.), 1; Tlalpán, 1. HIDALGO: Real del Monte, 1; Tula, 1. "Mexico" [= Real del Monte, Hidalgo], 1 (type).

2) COAHUILA: Carneros, 4; Diamante Pass (11 mi. S Saltillo, 7,800–9,600 ft.), 4; Sierra Encarnación, 5; Sierra de Guadalupe, 1.

Aphelocoma coerulescens sumichrasti (Baird and Ridgway)

Cyanocitta floridana, Sclater (1856:300), part.

Cyanocitta californica, Sclater (1858:302), part.

Aphelocoma californica, Salvin and Godman (1887:492), part.

Cyanocitta floridana var. *sumichrasti* Baird and Ridgway (1873:199), original description.
[Cyanocitta californica] var. *sumichrasti*, Baird, Brewer, and Ridgway (1874:283), part.
Cyanocitta sumichrasti, Baird, Brewer, and Ridgway (1874:283), part.
[Aphelocoma californica var. *woodhousei*] *d. sumichrasti*, Coues (1874b:219).
Aphelocoma floridana var. *sumichrasti*, Coues (1874b:219, in synonymy).
Aphelocoma sumichrasti, Sharpe (1877:114).
Aphelocoma californica sumichrasti, Oberholser (1917:95).
Aphelocoma coerulescens sumichrasti, Hellmayr (1934:55).

Type.—Adult specimen of unknown sex, no. 42149, USNM; Orizaba, Veracruz, Mexico; collected by F. Sumichrast, date unknown. My measurements of the type are as follows (mm.): wing, 140.7; tail, 147.0; bill length, 18.7; bill depth, 8.8; bill width, 8.0; tarsus, 40.5; hind toe, 13.1; middle toe, 20.5. The specimen is moderately worn and was probably collected in the spring months.

Nomenclatural history.—For several decades after their discovery in the mid-nineteenth century, scrub jays of southern Mexico were regarded as conspecific with the "species" *californica* (Selater, 1858; Salvin and Godman, 1887) primarily on the basis of certain superficial similarities which appeared striking when either form was compared with the geographically intervening, dissimilar "species" *woodhousei*. In 1873 Baird and Ridgway named the southern Mexican form "*sumichrasti*." Since then, the only taxonomic change affecting the concept of *sumichrasti*, per se, has been the geographic extension of *cyanoitis* southward (Ridgway, 1904:335) to include the state of México, earlier included in the range of *sumichrasti* (Baird, Brewer, and Ridgway, 1874:283).

Specimens examined.—Total, 32 (table 36). PUEBLA: Chalchicomula (8,700 ft.), 5; 8 mi. NE Chalchicomula (10,350 ft.), 1; Mount Orizaba, 2 (including type); Pinal, 1; San Martín, 2; Tehuacán, 1; Tochimilco, 2. TLAXCALA: Huamantla, 1. VERACRUZ: Perote, 1. OAXACA: Coixtlahuaca, 1; Ejutla, 2; Mount Zempoaltepec, 1; Nacaltepec, 1; 15 mi. W Oaxaca, 2; 5 mi. NE Cerro San Felipe (9,000 ft.), 8; Tlapancingo, 1.

Aphelocoma coerulescens remota Griscom

Aphelocoma californica remota Griscom (1934:392), original description.
Aphelocoma coerulescens [sic] remota, Berlioz (1937:174).

Type.—Adult female, no. 163815, MCZ; Chilpancingo, Guerrero, Mexico; collected by W. W. Brown, October 27, 1931 (Griscom, 1934:392; Peters, 1943:104). My measurements of the type are as follows (mm.): wing, 140.3; tail, 141.8; bill length, 17.6; bill depth, 9.0; tarsus, 42.2.

Nomenclatural history.—The first Guerreran specimens of the scrub jay to reach North American museums were apparently those taken by Nelson and Goldman in 1903 and deposited in the collections of the Biological Survey. Subsequently the American Museum acquired three specimens taken in 1899. The specimens in the Biological Survey collection were regarded by early students as representatives of "*sumichrasti*," but neither they nor the American Museum specimens were ever reported in the literature. In 1934, on the basis of newly acquired, ample material, Griscom described the Guerreran scrub jay as a distinct race of *californica*. Hellmayr (1934:55) only mentions this race in a footnote using Griscom's name, but intended, of course, that it be included in the *coerulescens* rassen-

kreis. Although not so strongly differentiated as Griscom maintained (see Berlioz, 1937: 175, and p. 309, *remota* is a clearly recognizable race.

Specimens examined.—Total, 78 (table 37). GUERRERO: Amojileca (25 km. W Chilpancingo, 6,000 ft.), 2; Chilpancingo, 50 (including type); mountains near Chilpancingo, 5; Cuapongo, 10; Ftalistatipa, 2; La Laguna, 1; Omilteme, 6; Zumpango, 2.

Aphelocoma coerulescens coerulescens (Bosc)

[C[orvus] floridanus Bartram (1791:286, 290).

Corvus coerulescens Bosc (1795:87), original description.

Garrulus cyaneus Vieillot (1817:476).

Garrulus coerulescens, Vieillot (1817:480).

P[ica] coerulescens, Wagler (1827); Pica, sp. 11.

Corvus floridanus, Bonaparte (1828a:58).

Garrulus floridanus, Bonaparte (1828b:59); Schlegel (1867:64, not of Bonaparte), part.

C[yanurus] floridanus, Swainson and Richardson (1831:495).

Cyanocorax floridanus, Bonaparte (1838:27).

[Cyanocitta] floridanus, Bonaparte (1850:377); Allen (1871:298, not of Bonaparte), part.

A[phelocoma] floridana, Cabanis (1851:221).

[Aphelocoma floridana var. *woodhousei*] *a. floridana*, Coues (1874b:219).

Aphelocoma cyanea, Coues (1899:84).

Aphelocoma coerulescens, Hellmayr (1930:132).

Aphelocoma coerulescens coerulescens, Hellmayr (1934:50).

Cyanocitta coerulescens, Amadon (1944a:3), part.

Cyanocitta c[oeulescens] coerulescens, Amadon (1944b:1).

Type locality.—North America; location of type unknown (Hellmayr, 1930: 132; 1934:50).

Type locality for *Corvus floridanus* Bartram proposed by Harper (1942:213) as "13 miles southwest of Palatka, between Rodman and Deep creeks, Putnam County, Florida."

Nomenclatural history.—Among the early names applied to the scrub jay of Florida, *Corvus floridanus* of Bartram (1791:290) antedates all others, but it has not been accepted by systematists because Bartram was not a strict binomialist. Opinion has differed on the advisability of adopting those Bartramian names which conform to Linnaean usage.

Bartramian names, revived by Coues (1875), were declared untenable by Allen (1876a), although the latter author soon afterward (1876b) agreed that those of Bartram's names which were identifiable and binomial were entitled to recognition. Two of these names, including *Corvus floridanus*, were used in the first two editions of the American Ornithologists' Union Check-list (1886, 1895); but a few years later, the A.O.U. Check-list Committee (1899:112) ruled that all names of Bartram were invalid because he was not a strict binomialist.

Recently, revival of Bartramian names has been proposed again by Harper (1942:210) and Merrill (1945:10). Harper's proposal appears cautious and selective; he points out that the identifiable names are accorded recognition by the International Rules of Zoölogical Nomenclature, in which no reference is made to names of authors who were not strict binomialists. As a matter of fact (see *Opinions* 20, 54), there is an implied acceptance of the fact that although certain authors may not be strict binomialists, their identifiable binomials are to be used.

Bartramian names are not, as stated by Harper (1942:211), "fully accepted" by botanists. (See Rickett, 1944:389.) On the basis of Article 68 in the International Rules of Botanical Nomenclature, quoted by Harper, all Bartramian names are void. Some Bartramian names are used by mammalogists and ichthyologists.

The only important events in the nomenclatural history of the Floridan form concern its relationship with western forms of the scrub jay. Schlegel (1867:69), Allen (1871:298), and Coues (1874b:219) had regarded "*floridana*" (= *coerulescens*), *woodhouseii*, and *californica* as conspecific. Excepting their views, the Floridan form was treated as a full species until 1934, when Hellmayr reduced all forms of the scrub jay to races of *coerulescens*—an action subsequently adopted by the A.O.U. Check-list Committee (1944:453).

Specimens examined.—Total, 212, divided as follows: (1) eastern Florida, west to Lake George and Orange County, 156 (table 38); (2) western Florida, east to Marion, Lake, and Highlands counties, 56 (table 39).

1) *Brevard County*: Merritt Island: Allenhurst, 8, mouth of Banana River, 5, Merritt, 3, Cape Canaveral, 5, opposite Titusville, 3, midway between Titusville and Cocoa, 1, Wilson, 8, Mosquito Lagoon (including Dummitt's), 3, and unspecified, 5; Eau Gallie, 21; Georgiana, 3; Grant, 2; Indianola, 2; Indian River, 5; Titusville, 2; unspecified, 1. *Indian River County*: Sebastian, 5. *Monroe County*: Key West, 1. *Palm Beach County*: Boynton, 1; Jupiter, 15; Lake Worth, 8; Lantana, 1; unspecified, 2. *St. Johns County*: Anastasia Island, 1; St. Augustine, 2; 10 mi. N St. Augustine, 2. *Volusia County*: Blue Springs, 22; Bulow, 1; Enterprise, 15; Holly Hill, 1; New Smyrna, 1; Ponce Park, 1.

2) *Gilchrist County*: Wannee, 3. *Glades County*: unspecified, 2. *Highlands County*: Lake Istokpoga, 2; 6 mi. E Sebring, 1. *Lake County*: Withlacoochee River, 1. *Lee County*: Alva, 4; Fort Myers, 2. *Levy County*: Cedar Keys, 14; Lukens, 4. *Manatee County*: unspecified, 2. *Marion County*: Oklawaha River, 1. *Pasco County*: Anclote, 3; Anclote River, 1. *Pinellas County*: Clearwater, 4; Dunedin, 1; John's Pass, 1; Seven Oaks, 1; Tarpon Springs, 5. *Sarasota County*: Miakka, 2; Sarasota, 1; Sarasota Bay, 1.

***Aphelocoma ultramarina arizonae* (Baird and Ridgway)**

Cyanocitta sordida (not *Garrulus sordidus* Swainson), Baird (1858:587), part.

[*Cyanurus*] *sieberi* (not *Pica sieberi* Wagler), Gray (1870:4), part.

[*Aphelocoma*] *sordida*, Coues (1872:166).

Cyanocitta ultramarina, var. *arizonae* Baird and Ridgway (1873:199), original description, part.

Cyanocitta sordida var. *arizonae*, Baird, Brewer, and Ridgway (1874: pl. 41).

Aphelocoma ultramarina . . . var. *arizonae*, Coues (1874a:129).

[*Aphelocoma sordida*.] Subsp. a. *Aphelocoma arizonae*, Sharpe (1877:117).

Aphelocoma sordida arizonae, Ridgway (1880:185).

Aphelocoma sieberi arizonae, Ridgway (1885:355).

Aphelocoma ultramarina (not *Corvus ultramarinus* Bonaparte), Salvin and Godman (1887:418), part.

[*Aphelocoma*] *arizonae*, Salvin and Godman (1887:494).

Type.—A first-year individual of unknown sex, no. 18279, USNM; Fort Buchanan (= Fort Crittenden), forty-five miles southeast of Tucson, Santa Rita Mountains, Santa Cruz County, Arizona; collected by Colonel Bernard J. D. Irwin, December 9 (1858?) (Baird and Ridgway, 1873:199; Bailey, 1923:33). Measurements of the type, which I have examined, are as follows (mm.): wing, 155; tail, 137; bill length, 19.5; bill depth, 9.8; bill width, 8.9; tarsus, 41.1; hind toe, 14.2; middle toe, 19.6. Base of upper mandible yellow, lower mandible yellow except distal halves of lateral surfaces.

Nomenclatural history.—Since this pale race was first distinguished from darker, east Mexican races in 1873 by Baird and Ridgway, all changes in its nomenclature have pertained to the specific rather than the racial name.

Specimens examined.—Total, 403, divided as follows: (1) southeastern Pima County and Santa Cruz County, Arizona, 88 (table 44); (2) Huachuca Mountains, southwestern Cochise County, Arizona, 100 (table 43); (3) Chiricahua Mountains, eastern Cochise County, Arizona, 74 (table 40); (4) Gila, southern Navajo, Pinal, Graham, northeastern Pima, and northwestern Cochise counties, Arizona, 44 (table 42); (5) southwestern New Mexico, 15; (6) northern Sonora, 41 (table 45); (7) northwestern Chihuahua, 41 (table 46).

1) *ARIZONA. Pima County:* Baboquivari Mountains (Thomas Canyon, 4,000–5,000 ft.), 11; 28 mi. SE Tucson (Cochi Canyon), 1; Rosemont, 1; Santa Rita Mountains: 10 mi. SE Continental, 1, Florita Canyon (4,000 ft.), 1, and Sawmill Canyon (4,000 ft.), 4. *Santa Cruz County:* Atasco Mountain (Piskorski Canyon, 4,500 ft.), 2; Nogales, 1; Pajarito Mountains (= Oro Blanco Mountains): Sycamore Canyon (4,000 ft.), 3, and unspecified, 1; Patagonia, 1; 7 mi. N Patagonia (4,500–4,800 ft.), 8; 4 mi. S Patagonia (3,800 ft.), 2; 5 mi. SE Patagonia (4,500 ft.), 1; 4–5 mi. W Patagonia (5,000 ft.), 3; 7 mi. E Patagonia, 1; Patagonia Mountains (Guajalote Flat, 5,000 ft.), 2; San Rafael Valley, 1; Santa Rita Mountains: Fort Crittenden (= Fort Buchanan, 4,700–5,000 ft.), 10 (including type), and Madera Canyon (4,400–6,000 ft.), 30; Tumacacori Mountains: Piña Blanca Spring, 2, and 2 mi. E Piña Blanca, 1.

2) *Cochise County:* Huachuca Mountains: Carr Canyon, 1, Palmerlee, 8, and unspecified, 91.

3) *Cochise County:* Chiricahua Mountains: Paradise (5,500 ft.), 27, Pinery Canyon (5,000–7,500 ft.), 28, Portal (5,000 ft.), 4, Bucker Canyon, 1, Turkey Canyon, 1, Whitetail Canyon (5,000–5,100 ft.), 2, and unspecified, 11.

4) *Gila County:* Near Cazador Spring (S slope Natanes Plateau, 4,700 ft.), 1; 25 mi. NE Rice (5,800 ft.), 1; Sawmill (27 mi. NE Globe, 5,600 ft.), 12; Sierra Ancha: Carr's Ranch (5,410 ft.), 3, Workman Creek, 1, and unspecified, 8. *Pinal County:* Catalina Mills, 2; Oracle, 3; unspecified, 1. *Pima County:* Santa Catalina Mountains, 2. *Graham County:* Ash Creek (6,100 ft.), 4; Graham Mountains, 1. *Cochise County:* Dragoon Mountains, 2; Rincon Mountains, 3.

5) *NEW MEXICO. Grant County:* Burro Mountains, 1; Copper Mines (= Fort Webster), 1; Fort Bayard, 1; Gila River, 1; Santa Rita, 1; 2 mi. W Santa Rita (6,300 ft.), 1; Silver City, 4; 2½ mi. N Silver City, 1. *Hidalgo County:* Animas Mountains (Animas Peak, 5,800–6,000 ft.), 3; San Luis Mountains, 1.

6) *SONORA:* Río de Bavispe, 1; Casita (40 km. S Nogales, 3,300 ft.), 10; Cibuta, 2; Cuchuta, 1; La Chumata, 2; Dos Cabezas, 1; Nogales, 1; San José Mountains, 10; Sáric, 10; Sierra Charuco (Arroyo Texas, 3,000–3,500 ft.), 4; Sierra de los Patagones, 2; Sierra de Guadalupe (Guadalupe Canyon, 4,500 ft.), 1.

7) *CHIHUAHUA:* Bustillos, 5; Cajón Creek, 1; Colonia García, 4; Colonia Juárez, 1; Colonia Pacheco, 1; 30 mi. W Miñaca, 7; Mojarachie (6,900 ft.), 5; Pacheco, 1; Río Gavilán (7 mi. SW Pacheco), 10; 7 mi. W Sauz (29°02' N, 106°23' W, 5,750 ft.), 1; Tamarino, 1; unspecified, 4.

Aphelocoma ultramarina wollweberi Kaup

Cyanocitta ultramarinus (not *Corvus ultramarinus*), Bonaparte (1850:378; see van Rossem, 1942b:573).

Aphelocoma wollweberi Kaup (1854:lv), original description, part.

Aphelocoma couchi, G. S. Miller (1896:36), part.

Aphelocoma sieberii wollweberi, Ridgway (1904:341), part.

Aphelocoma soraida wollweberi, Hellmayr (1934:56), part.

Aphelocoma ultramarina wollweberi, van Rossem (1945:178).

Type.—Unknown; the original specimen was obtained in Zacatecas, Mexico, by Wollweber.

There is an adult specimen, sex unknown, no. 5250, in the collection of the

Brussels Museum, obtained for Kaup by Wollweber in Zacatecas and sold by Kaup to the Brussels Museum. This specimen may be a co-type or even the type. According to van Rossem (MS), it is a "mounted bird in excellent condition; . . . fully adult by plumage; collected probably in late winter or early spring to judge by amount of abrasion. Central pair of rectrices distinctly shorter (5 mm) than the next pair; under side of all save central rectrices obsoletely barred (inner webs only) in certain light, the barring and interspaces about = and about 2 mm wide. This specimen is registered (under 'var Couchi') as '5250, Mexique (ach. Kaup sous le nom de wollweberi Kp.)'" (van Rossem, MS). Van Rossem's measurements of this specimen are as follows (mm.): wing, 157; tail, 129; exposed culmen, 25.4; depth of bill at base, 9.0; tarsus, 38.0; middle toe without claw, 20.0. Unfortunately, no data are available on the color of this specimen; these are particularly desirable because of the overlap in measurements of *A. u. wollweberi* (table 49) and *A. u. sordida* (table 54) which probably occurs in eastern Zacatecas.

One detail in Kaup's (1854:lv) original description of *wollweberi* agrees with the data provided by van Rossem: both Kaup's bird and specimen no. 5250 are stated to have the central pair of rectrices shorter than the neighboring pair. This occurs so infrequently in *adult* specimens that the agreement may be more than coincidence.

Nomenclatural history.—A small, pale race of *A. ultramarina* from the southern Sierra Madre Occidental was described by G. S. Miller in 1896 as *Aphelocoma gracilis*, but soon thereafter that name was replaced by an earlier one, *Aphelocoma wollweberi* of Kaup (1854). The latter name has been in use since the publication of Ridgway's (1904) monograph, in which (p. 342) the original description is quoted.

In the light of all data now available, it seems to me that Kaup's name may apply to either *sordida* or *wollweberi* of this monograph. Kaup's statement (1854:lv) that *wollweberi* "ist weniger intensiv blau" could apply as well to *sordida* as to the form occurring in western Zacatecas and Durango when either is compared with his "*Sieberi*" (= *ultramarina*). Kaup's further phrase, "mit röthlich grauem Rücken," is the best basis for associating his "*Wollweberi*" with the grayer race of western Zacatecas and Durango. But if one makes the comparison made by Kaup, namely, that of "*Sieberi*" with either *sordida* (his "*Ultramarina*"?) or *wollweberi*, and if one uses specimens worn moderately or more, Kaup's phrase can apply to either of the smaller races.

The unquestioning acceptance of Kaup's name by Ridgway and Hellmayr is a puzzle to me. Critical scrutiny of wording and factual content of Kaup's description brings up one question after another, but a discussion of them seems futile because no definite type exists. It is worth while, however, to record a transcription of his measurements. These are based on the Parisian foot, which is equal to

	Length	Bill	Wing	Tail
" <i>Wollweberi</i> "	271	29 3	147	120-129
" <i>Ultramarina</i> "	298	29.3	156	120-129
" <i>Sieberi</i> "	352	29.3	185	183

0.325 meters. Subdivisions of the inch (") used by Kaup are lines (') (1"=12'). The dimensions (mm.) given by him (1854:lv) are presented in the table (p. 409).

His "*Sieberi*" is *ultramarina* of this monograph. But his "*Ultramarina*" is certainly something else, possibly *sordida* of this monograph, as not even the smallest first-year female of *ultramarina* fits these measurements. Judging by the wing measurement, both "*Wollweberi*" and "*Ultramarina*" could apply to *sordida* or *wollweberi* in the present study. Without knowledge of the age and sex of the specimens, especially the age, it is not possible to draw any definite conclusions.

Thus I cannot agree with Hellmayr (1934:56) that with "little doubt . . . *wollweberi* is an earlier name for *A. gracilis*." It is not clear to me that "Kaup's description . . . fits" the form of western Zacatecas, or what was considered to be the same as G. S. Miller's *gracilis*. Moreover, his assertion that the type localities of *wollweberi* (Zacatecas) and *gracilis* (Sierra Bolaños, northeastern Jalisco) are "in the same section of the central Mexican tableland" denies the possibility that within the large state of Zacatecas (exclusive of the northeastern part, to which he attributes *sordida*) two races might occur. Ridgway (1904:342) simplified the problem of applying Kaup's name by stating that the range of *wollweberi* extends into "western San Luis Potosí." To my knowledge there is no basis for this extension. Hellmayr followed Ridgway and apparently confused *sordida* with *wollweberi*, as is evident from his statement that *wollweberi*, or the west-central Mexican race, is "very doubtfully separable from typical *sordida*," or the east-central Mexican race. These are as distinct from each other as other pairs of closely related races the status of which is not questioned by Hellmayr.

It may be noted that when Miller (1896:35) described *Aphelocoma gracilis*, he compared that form with a series of specimens mainly from San Luis Potosí which he placed under the name "*Aphelocoma couchi*." All the specimens of the latter series he found to be darker and larger than *gracilis*. Included by Miller in that series was one from Jerez in central Zacatecas which proved to be the largest of the adult males. The color of the Jerez specimen, which I have examined, is not, as Miller maintained, representative of "*couchi*" or *sordida*, but the comparative measurements given by him correctly emphasize differences between *gracilis* and his "*couchi*," which includes the Jerez specimen. It should be understood that three races are involved in this problem, whereas Hellmayr thought there were only two and possibly just one. (See above.) But I emphasize the details because, to my mind, Miller's evidence was not given due consideration. It contradicts Hellmayr's statements and indicates that there certainly are two distinguishable races in the area of Zacatecas and neighboring parts of Jalisco and San Luis Potosí. Hellmayr's treatment of the relationships of *wollweberi* and *sordida* is inconclusive, and his opinions cannot be appraised satisfactorily without locality data for all the "five specimens" of his *wollweberi* which he examined.

It is probable that *sordida* occurs in eastern Zacatecas, but no specimens are available from that part of the state. *Wollweberi* is known to occur as far east as Jerez. Under these circumstances the name *wollweberi* might apply either to the west-central or the east-central race. But there is no justification for a change in the present usage of that name, since no definite type is available. Elsewhere (p. 330) I have restricted the type locality of *wollweberi* to the Valparaíso Moun-

tains, the northwesternmost locality within Zacatecas from which I have examined specimens. This locality is thus closer to the main geographic area of *wollweberi*, as heretofore known, than other Zacatecan localities.

Specimens examined.—Total, 88, divided as follows: (1) extreme southeastern Sonora, southwestern Chihuahua, northwestern Sinaloa, and Durango, 75 (table 48); (2) Zacatecas and northeastern Jalisco, 13 (table 49).

1) SONORA: 20 mi. NE Guiracoba (5,000 ft.), 2; Mina Abundancia (see van Rossem, 1934: 425), 15; Sierra Charuco (Arroyo Texas, 3,000–3,500 ft., 27°30' N), 4. CHIHUAHUA: Bravo, 12; Carmen, 1; Jesús María, 2. SINALOA: Pinos Gordos, 2; Sierra de Choix (NE Choix), 3. DURANGO: Arroyo de Buey, 1; Ciénaga de las Vacas (8,500 ft.), 15; Coyotes, 1; 25 km. S Durango (6,800 ft.), 1; 30 mi. SW Durango, 1; El Salto, 4; La Boquilla, 2; Laguna del Progreso (90 mi. NW Durango), 1; La Providencia, 4; Las Bocas (6,800 ft.), 4.

2) ZACATECAS: Jerez, 1; Monte Escobedo, 1; Plateado, 3; Sierra Madre, 2; Valparaíso Mountains (restricted type locality), 3. JALISCO: Florencio, 1; Colotlán, 2.

Aphelocoma ultramarina gracilis G. S. Miller

Aphelocoma gracilis G. S. Miller (1896:34), original description, part.

Aphelocoma sieberi wollweberi, Ridgway (1904:341), part.

Aphelocoma sordida wollweberi, Hellmayr (1934:56), part.

Type.—Adult male, BM, no. 5658 in the collection of Gerrit S. Miller, Jr.; Sierra Bolaños, Jalisco; collected by W. B. Richardson, February 26, 1889 (G. S. Miller, 1896:34). Measurements of the type (*ibid.*:37) are as follows (mm.): wing, 146; tail, 138; length of bill from nostril, 20; depth of bill through nostril, 8.8; tarsus, 33.

Nomenclatural history.—G. S. Miller's name, *gracilis*, long regarded as a synonym of *wollweberi* (see p. 330), is here revived, since specimens from Nayarit and north-central Jalisco prove to be distinguishable from *wollweberi*, *sensu stricto*, of Durango. (See p. 410.)

Specimens examined.—Total, 15 (table 50). JALISCO: near Bolaños (type locality), 11. NAYARIT: R[ancho] de Buenavista, Sierra de Nayarit, 2; Santa Teresa, 2.

Aphelocoma ultramarina couchii (Baird)

Cyanocitta ultramarina (not *Corvus ultramarinus* Bonaparte), Baird (1858:588).

[*Cyanocitta*] *couchii* Baird (1858:588), original description, part.

[*Cyanurus*] *ultramarinus*, Gray (1870:4), part.

[*Cyanocitta*] *sordida* (not *Garrulus sordidus* Swainson), Selater and Salvin (1873:39).

[*Cyanocitta ultramarina*] var. *couchii*, Baird, Brewer, and Ridgway (1874:284), part.

[*Aphelocoma ultramarina*.] Subsp. n. *Aphelocoma couchii*, Sharpe (1877:116).

Aphelocoma ultramarina couchii, Ridgway (1880:185).

Aphelocoma ultramarina, Salvin and Godman (1887:493), part.

[*Aphelocoma*] *couchii*, Ridgway (1887:357); G. S. Miller (1896:36, not of Ridgway), part.

Aphelocoma sieberi couchii, Oberholser (1902:300).

Aphelocoma sieberi potosina Nelson (1899a:27), part.

Aphelocoma sordida couchii, Hellmayr (1934:56), part; Burleigh and Lowery (1942:196, not of Hellmayr).

Aphelocoma sordida sordida, Hellmayr (1934:56), part.

Type.—First-year male, no. 4113, USNM; Guajuco, eighteen miles southeast of Monterrey (not at "Monterey"), Nuevo León; obtained by Lieutenant D. N. Couch, April, 1853; orig. no. 157 (Baird, 1858:588; G. S. Miller, 1896:35, 37).

Measurements of the type, which I have examined, are as follows (mm.): wing, 144; tail, 126; bill length from nostril, 18.9; bill depth, 8.8; bill width, 8.3; tarsus, 90.1; hind toe, 15.1; middle toe, 20.6. The specimen is worn and soiled; it is a first-year individual, not an adult, as Miller stated (*ibid.*: 37), and is grayer than adults collected at the same time of year.

Nomenclatural history.—Since *couchii* was first named by Baird in 1858, and since its range was first defined by Ridgway in 1904, no change occurred in the use of this name until 1942, when Burleigh and Lowery, without word of explanation, applied *couchii* to specimens from southern Coahuila, an area included in the range of the neighboring race *potosina* or *sordida* by Ridgway (1904:340) and Hellmayr (1934:57). This southward extension of the range of *couchii* has been confirmed by results reported in this paper.

Specimens examined.—Total, 189, divided as follows: (1) Brewster County, Texas, and northern Coahuila, 90 (table 51); (2) southern Coahuila and central Nuevo León, 51 (table 52); (3) southern Nuevo León and west-central Tamaulipas, 48 (table 53).

1) TEXAS. *Brewster County*: 5 mi. W Alpine (5,300 ft.), 1; Chisos Mountains: Blue Creek (6,900–7,000 ft.), 4, Boot Spring (6,500–6,700 ft.), 9, N of Emery Peak (5,100–5,500 ft.), 3, near Headquarters, Big Bend Park, 1, Juniper Canyon, 1, Upper Juniper Spring (5,000 ft.), 5, Wade (or Pine) Canyon, 19, and unspecified, 44. COAHUILA: Las Cruces, 3.

2) COAHUILA: Carneros, 2; Diamante Pass, Saltillo (7,000–7,500 ft.), 3; Sierra de Guadalupe, 4; Viboras Canyon, 1. NUEVO LEÓN: Boca Negro, 2; Diente Mountain (near Monterrey), 2; Cerro de Potosí (7,000 ft.), 3; Cerro de la Silla ("Saddle Mountain"), 2; 3 mi. S Galeana, 1; Guajeco (18 mi. SE Monterrey), 2 (including type); Horsetail Falls (near Santiago, SE Monterrey), 1; 14 mi. SW Linares, 1; Mesa del Chipinque (10 mi. SW Monterrey), 9, and (at 4,000 ft.), 5; San Pedro Mines, Camp 2, 6; 15 mi. SW Villa Santiago, 1; unspecified, 6.

3) NUEVO LEÓN: Boquillo, 3. TAMAULIPAS: Carricitos, 1; Ciudad Victoria, 2; Galindo, 7; Juamave, 1; 15 mi. S Juamave La Jolla (5,000 ft.), 2; Miquihuana, 15; Rampohuato, 1; Realito, 5; Santa Leonar, 1; La Victoria (including Sierra Madre, Victoria), 10.

Aphelocoma ultramarina sordida Swainson

Garrulus sordidus Swainson (1827:437), original description, part.

[*Cyanurus*] *sordidus*, Swainson and Richardson (1831:495), part.

†*Cyanocitta sordida*, Duges (1870:139).

Aphelocoma ultramarina, Salvin and Godman (1887:493), part.

Aphelocoma couchi, G. S. Miller (1896:86), part.

Aphelocoma sieberi potosina Nelson (1899a:27), part; Ridgway (1904:340, not of Nelson), part.

Aphelocoma sieberi wollweberi, Ridgway (1904:341), part.

Aphelocoma sordida wollweberi, Hellmayr (1934:56), part.

Aphelocoma sordida sordida, Hellmayr (1934:56), part.

Type.—An unnumbered adult specimen of unknown sex, in the collections of Cambridge University, England, is identified as the type by van Rossem (1939: 86). Details concerning this specimen have been published by him (*ibid.*) and by Brodkorb (1944:400). Van Rossem's (MS) measurements (mm.) of the "type" are as follows: wing, 175; tail, 158; tarsus, 45. A tag borne by this specimen reads "Garrulus sordidus Sw. / Bullock Mexico." Van Rossem notes further: "In [Swainson's 1832] publication, he is specific about having only one specimen [and] there cannot be more than a holotype. . . . The Cambridge specimen supplies measurements almost exactly as given by Swainson in Zool. Illustr. [1832] and is unquestionably the type. . . . Very dirty below—hence '*sordidus*.'"

Nomenclatural history.—Swainson's *Garrulus sordidus*, the first of two names (Hellmayr, 1934:57) applied in 1827 to the species named *Corvus ultramarinus* by Bonaparte in 1825, had been set forth repeatedly as the correct name for the ultramarine jay of southeastern Mexico until 1877, when Sharpe last used it. Subsequently it was dropped in favor of *Pica sieberii* Wagler, apparently because of certain discrepancies in Swainson's descriptions (van Rossem, 1939:86) and because of doubtful priority of *Garrulus sordidus* over *Pica sieberii*. Ridgway (1904:339) listed *Garrulus sordidus* in the synonymy of his *A. sieberii sieberii*, even though the type locality, Real del Monte, which he mentions, falls into the range of his *A. s. potosina*. He offered no explanation.

In 1934 Hellmayr adopted *Garrulus sordidus* as an earlier name for *A. s. potosina* of east-central Mexico, named by Nelson in 1899. His basis for this action apparently was the fact that Real del Monte falls between Hidalgo localities listed by Ridgway (1904:340) in the statement of range for *potosina* (but see beyond). After examining the type of *Garrulus sordidus*, van Rossem (1939:86) concluded that it was representative of the southeastern race, and reversed Hellmayr's action. Van Rossem's observations, however, left open a question of type locality.

Swainson (1827:437) originally gave Real del Monte, Hidalgo, as the type locality of *sordidus*, but later (1832:text to pl. 36) stated that it "inhabits the table land of Mexico, from whence our specimen was received." This later statement has been construed by Brodkorb (1944:401) as a revocation of Swainson's earlier, more specific locality. The supposition that Swainson had made an error was strengthened, according to Brodkorb, by the argument that "specimens from Hidalgo belong to the small subspecies separated by Nelson as *Aphelocoma sieberii potosina*" (Brodkorb, *ibid.*) and by the fact that according to van Rossem (1939:86) Swainson's type is representative of the southern plateau race. Brodkorb points out that Bullock (1824:445) mentions having obtained "two kinds of blue jays, all undescribed," near Río Frío in the state of México, and concludes that these are *Garrulus sordidus* and *Garrulus coronatus* of Swainson (1827:437). Swainson supposedly had but one specimen of *Garrulus sordidus*. On the basis of this evidence Brodkorb proposed to restrict the type locality of *sordidus* to Río Frío, state of México.

I do not recognize van Rossem's contentions as adequately proved nor Brodkorb's action as valid, and I retain the name *sordida* for Nelson's *potosina* for four reasons. First, Nelson's *potosina* from San Luis Potosí represents a segment of a size cline along the Sierra Madre Oriental, the large extreme of which is apparently located in central or central-southern Hidalgo. One adult male from El Chico (wing, 172 mm.) falls at the upper limit of variation among specimens from San Luis Potosí and northern Hidalgo. Hidalgo specimens will probably prove to average larger than San Luis Potosí specimens. Normal variation would be expected to include the measurements of 175 mm. for the wing and 158 mm. for the tail of the "type" of *Garrulus sordidus* given by van Rossem (1939:86), if it is an adult. Mr. J. D. MacDonald of the British Museum has kindly examined Swainson's specimen, and his report clearly indicates that it is an adult. If the type had proved to be a first-year bird, the measurements would then have strengthened van Rossem's contention that the Cambridge specimen represents *A. u. ultramarina* and, by implication, that it probably did not come from Real del Monte.

Second, some real doubts now exist in regard to the color of the type. The El Chico specimen mentioned above is clearly representative of the lighter, less purplish race of San Luis Potosí and in no way suggests intergradation with *ultramarina*. Specimens from Real del Monte, only a few miles southeast of El Chico, would not be expected to differ in color. (See p. 340.) As to the color of the type, van Rossem (1939:86) provides no specific data except to say that it is "dirty below." This would indicate that dorsal coloration is also dirty. If the latter is true, the resulting coloration would be abnormally purplish, depending in degree on the amount of wear—an effect which I have noted in specimens of *A. c. woodhousei* collected in mining districts. Thus, color of the type must be judged by comparisons with specimens of comparable wear from northern Hidalgo or San Luis Potosí, on the one hand, and others from Veracruz, Puebla, or México, on the other hand, and due allowance must be made for discoloration.

Third, there seems to be no good reason for doubting that Swainson had a specimen of *A. ultramarina* actually collected at Real del Monte. Of 102 species listed by him in his 1827 synopsis of the Bullock collection, 20 are reported from Real del Monte. Bullock does not mention that locality; presumably he did not visit Real del Monte, but obtained specimens from there from someone, possibly the Mr. Morgan mentioned by Swainson (1827:366). Species recorded at Real del Monte include "*Pyrranga hepatica*," "*Fringilla socialis*," "*Colaptes mexicanus*," and "*Sialia azurea*," which might be expected to occur in pine woodland of the type inhabited by *A. ultramarina*.

Fourth, there is no conclusive evidence whereby Swainson's specimen of *Garrulus sordidus* might be identified as one of the two blue jays obtained near Río Frío. It has been assumed that Bullock's specimens passed into Swainson's hands and that Swainson had but one specimen of his *Garrulus sordidus*, but these assumptions do not seem to me to have been adequately justified in the literature on this problem. There is no indication in his 1827 paper whether he had one or more specimens. If it is assumed that he had but one, it must be assumed further that he had exactly one of all other species for which he provides measurements! In his later work he states (1832: pl. 86), "The *Garrulus sordidus* inhabits the table land of Mexico, from whence our specimen was received." Why cannot "our specimen" refer to the figured one? Also, the discrepancies between his 1827 and 1832 measurements seem to be unexplained by the suggestion that they are mere errors. The measurements (inches) are given in the table. Only the tail measurements are the

	1827	1832
Total length.....	11	14
Bill.....	1½	1½
Wings.....	6½	7
Tail.....	6½	6½
Tarsi.....	1½	1 7/10

same. The difference in lengths seems too large to have been an error. Errors of this magnitude are, of course, not rare in early works of avian systematics, but who can prove that four out of the five earlier measurements were erroneous? My

main point is that Swainson could have had more than one specimen and that the Cambridge specimen may not be the holotype.

Several days after the preceding paragraphs were written, I discovered a statement made by Baird (1858:588) to the effect that the type of *Pica sieberii* Wagler was the same as that of *Garrulus sordidus* Swainson. Actually, when Wagler described *Pica sieberii*, he had at least two specimens, one of which belonged to Leadbeater. (See p. 418; also Hellmayr, 1934: 57.) Wagler apparently obtained his specimens through Leadbeater after the Bullock Museum containing specimens studied by Swainson was dispersed. Wagler's description of *Pica sieberii* appeared in 1827, as did Swainson's description, but probably several months after the latter and almost certainly not before it (Hellmayr, *ibid.*). Thus, if one of Wagler's specimens was that described by Swainson, it is highly improbable that the specimen described by Swainson in 1832 is the same as the one described in 1827. The discrepancies in measurements discussed above support this contention. I do not support the claim of Baird that the two types were identical, but introduce this evidence as basis for deciding whether Swainson's 1827 and 1832 specimens were one and the same. My conclusion is that Swainson had more than one specimen in 1827 or obtained another of the same species between 1827 and 1832. At any rate, I cannot subscribe to van Rossem's (1939:86) contention that "there can be no co-types and the specimen in the collection at Cambridge must be regarded as the type." In my opinion, it is not the type.

In the British Museum there is an unsexed, fresh-plumaged adult (no. 1887: 3:9:53) of *A. u. ultramarina* from Jalapa, Veracruz, the label of which bears the following comment: "A little paler below and the tail rather more rounded than type of *Garrulus sordidus*, Sw. Otherwise the same. Comp'd 7. Mar 1887 O.S." I have examined this specimen. Its wing and tail measure 178 and 166 mm., respectively. It throws no light on the question of validity of the supposed type of *Garrulus sordidus*.

Thus the available evidence on the application of Swainson's name is too inconclusive for me to reject the type locality of Real del Monte. The measurements given by van Rossem do not prove that the Cambridge specimen represents *A. u. ultramarina*, even if it were the type, and nothing precise is known about its color. Finally, there is basis for doubt that Swainson had only one specimen. I would propose, therefore, that, pending acquisition of further sound evidence, the use of the name *sordida* be determined solely by the type locality, irrespective of the final decision on the racial identity of the Cambridge specimen. The entire problem is, of course, aggravated by the fact that Real del Monte falls close to the boundary between *sordida* and *ultramarina*.

Although my use of the name *sordida* agrees with that of Hellmayr (1934:56), I do not agree with his reason for that use. He states, "*A. s. potosina* is obviously typical *sordida*. . . . Birds from Tulancingo in that state, thus nearly topotypical, cannot be distinguished from others taken at Villar [in San Luis Potosí], which doubtless represent *potosina* of Nelson." On the basis of the specimens which I have examined, I cannot see how he arrived at this conclusion. (See p. 340.) Although my specimens are few in number, the observed differences do not warrant any conclusion other than that the Tulancingo specimens are representative of *A. u. ultra-*

marina. Real del Monte, the type locality of *Garrulus sordidus*, is closer to El Chico in central Hidalgo, where "*potosina*" occurs, than to Tulancingo in the southeastern part of the state. It is probable that Hellmayr was merely following Ridgway (1904:340), who also assigned Tulancingo specimens to the more northern race, his *potosina*; my comments apply with equal weight to his statements.

The race of east-central Mexico, to which the name *sordida* is applied here, was first described by Nelson in 1899 under the name *A. sieberi potosina*. From 1899 to 1934, when Hellmayr brought forth the use of *sordida*, no major change occurred in its nomenclature except that Ridgway (1904:340) departed from Nelson's original geographic delimitation of *potosina* by excluding eastern Zacatecas and Querétaro and including Hidalgo.

The type of Nelson's *potosina* is an adult male, no. 144642, Fish and Wildlife Service Collection, USNM, collected in mountains near Jesús María, San Luis Potosí, by E. W. Nelson, September 3, 1892, orig. no. 333 (Nelson, 1899a:27). Dimensions of the type, which I have examined, are as follows (mm.): wing, 168; tail, 145; bill length, 20.9; bill depth, 10.7; tarsus, 42.9.

Specimens examined.—Total, 28 (table 54). SAN LUIS POTOSÍ: Alvarez, 4; 5 mi. NE Ciudad del Maíz (5,000 ft.), 3; near Jesús María, 5 (including type); Villar, 5. HIDALGO: El Chico, 1; Jacala (including mountains to north and La Placita), 5; 6 mi. NE Jacala, 1; 7 mi. S Jacala, 1; 40 km. S Jacala, 1; Maguey Verde, 8½ mi. NE Zimapán, 1; 15 mi. N Remedios, 1.

Aphelocoma ultramarina ultramarina (Bonaparte)

Corvus ultramarinus Bonaparte (1825:387), original description (see van Rossem, 1942b:572).

Garrulus sordidus Swainson (1827:437), part.

P[ica] sieberii Wagler (1827:[332]).

Garrulus ultramarinus, Temminck and Laugier (1827:pl. 439).

Corvus asureus (not of Temminck, 1822) Lichtenstein (1830:1).

[*Cyanurus*] *sordidus*, Swainson and Richardson (1831:495), part.

O[yanooitta] ultramarina, Strickland (1845a:260).

O[yanooorax] sieberii, Gray (1849:307).

[*Cyanooitta*] *sieberi*, Bonaparte (1850:378).

A[phelocoma] sieberti, Cabanis (1851:221).

A[phelocoma] ultramarina, Cabanis (1851:221); Salvin and Godman (1887:493, not of Cabanis), part.

Oyanooorax ultramarinus, Selater (1857:204).

Cyanooitta sordida, Baird (1859b:pl. 22).

[*Cyanurus*] *sieberti*, Gray (1870:4), part.

[*Cyanurus*] *ultramarinus*, Gray (1870:4).

[*Cyanooitta ultramarina*] var. *sordida*, Baird, Brewer, and Ridgway (1874:284).

[*Cyanooitta ultramarina*] var. *ultramarina*, Baird, Brewer, and Ridgway (1874:284).

Aphelocoma sordida, Sharpe (1877:116).

Aphelocoma sieberti sieberti, Ridgway (1904:338), part.

Aphelocoma sieberti potosina, Ridgway (1904:340), part.

Aphelocoma sordida sordida, Hellmayr (1934:56), part; van Rossem (1939:86, not of Hellmayr).

Aphelocoma sordida sieberti, Hellmayr (1934:57), part.

Aphelocoma ultramarina ultramarina, Brodkorb (1944:400).

Type.—Not known definitely; sent to Bonaparte by Samuel M'Clellan from Mexico; type locality restricted to Temascaltepec, state of México, by van Rossem (1942b:578).

One of two unnumbered specimens in the Rijksmuseum van Natuurlijke Historie at Leiden examined and described by van Rossem (1942b:572) may be the actual type. The following data pertaining to this specimen are taken from van Rossem's original manuscript notes: "Mounted bird in good condition, plumage showing a slight amount of abrasion; evidently collected in spring. No sex indicated; definitely a one-year-old bird as shown by the relatively narrow, pointed rectrices. Mounted length 13¾". Bill slightly more prominently hooked at tip than shown in plate [see beyond]. . . . Temminck's plate matches exactly in detail of white exposed edge of left wing, but coloration of plate much too pale and too blue." The stand of this specimen bears the following information: "Cat. N° 1 / Garrulus ultramarina BP. / indiv. fig. Pl. col. 439 / indiv. type de la Cyanocitta Sieberi de Bonaparte / Cons. 1, p. 378 / Mexique." Van Rossem's measurements (mm.) are as follows: wing, 181; tail, 172; length of bill from nostril, 21.5; depth of bill at nostril, 11.2; tarsus, 42.4; middle toe without claw, 22.8; graduation of tail, 20.

This specimen was figured as "*Garrulus ultramarinus*. C. Bonap." by Temminck and Laugier (1827:pl. 439) and was the basis for Bonaparte's description of *Cyanocitta sieberi* in his *Conspectus generum avium* (1850:378), not of *Cyanocitta ultramarinus* of the same work (Schlegel, 1867:64; van Rossem, 1942b:573). Contrary to Ridgway (1904:339), this specimen is not the type of *Pica sieberii* Wagler; and, contrary to Brodkorb (1944:401), it cannot be said to be *the* (italics mine) type of Bonaparte's *Corvus ultramarinus*.

The second specimen present in the Rijksmuseum at Leiden is the basis of Bonaparte's description of *Cyanocitta ultramarinus* of 1850 (p. 378), but not of *Corvus ultramarinus* of 1825 (Schlegel, 1867:64; van Rossem, 1942b:573). The following data are provided by van Rossem's original manuscript notes: "Mounted bird in good condition; midwinter or perhaps early spring plumage. Mounted length 11 inches. Fully adult as shown by wing and tail feathers, no sex indicated." The bottom of the stand bears the following information: "Cat N° 2 / Garrulus ultramarinus, Bonap. / 33 Mexique." Van Rossem's (1942b:572) measurements are as follows (mm.): wing, 165; tail, 138; length of bill from nostril, 20.5; depth of bill at nostril, 10.1; tarsus, 42.0; middle toe minus claw, 13; graduation of tail, 13 mm. This specimen is stated by van Rossem (*loc. cit.*) to be "an example of the small race later named by Kaup as *Aphelocoma wollweberi*." The data on size provided by van Rossem do not prove conclusively that this specimen represents Kaup's race; it could be either *sordida* or *wollweberi*. Data on color are absolutely necessary before the identity of this bird can be settled. Van Rossem (letter of November 19, 1945) comments on it as follows: "Back grayer than head. Small bill. Pale coloration. This is not *potosina*."

Nomenclatural history.—The ultramarine jay of southeastern Mexico received three names in the years 1825 and 1827. The synonymy given above, limited to the earliest citation for each name, indicates only in part the comparatively hectic nomenclatural history of the large, dark race now called *A. u. ultramarina*.

The earliest of the three names, *Corvus ultramarinus* Bonaparte, had been rejected a number of times because one of the characters attributed to that species by Bonaparte (1825:387) was a "perfectly even" tail tip. Recently van Rossem (1942b:572) has examined specimens used as a basis for descriptions in a later

work of Bonaparte (1850) and has shown that Bonaparte's use of the word "even" should be taken in a comparative rather than a literal sense. Other details of Bonaparte's description indicate that the name applies to the southeastern race, *sieberii* of Ridgway (1904:338) and Hellmayr (1934:57).

The second of the three names, *Garrulus sordidus* Swainson (1827), is discussed on page 412. Since the greater part of the Mexican "table land" from which Swainson received specimens falls within the range of *ultramarina* and not *sordida*, this name must apply in part to the former race. *Sordida* is used for the east-central Mexican race because the type locality given by Swainson (1827) falls within the range of that race and because there is doubt that the Cambridge specimen of *Garrulus sordidus* is actually the type.

The third name, *Pica sieberii* Wagler (1827), used for the southeastern race since the turn of the century, is now replaced by *ultramarina*. The type of *Pica sieberii* Wagler (1827:sp. 23) is not known. A co-type in the Munich Museum (no. A103) was examined by van Rossem (MS) in August, 1933. According to van Rossem, it is a "skin in very poor condition, taken down from mount. There are three tags on this bird:—an old green one reading 'Cyanocorax Sieberii Wagler. Mexico,' a new white tag of the museum and a red type tag, the word Type having been changed to Co-type." His measurements of this specimen are as follows (mm.): wing, 184; tail, 171; exposed culmen, 28.8; depth of bill, 12.0; tarsus, 41.5. It is an adult, but sex is not indicated. Hellmayr (1934:57) refers to this specimen as "the author's [Wagler's] original specimen." The actual type apparently was contained in the collection of Leadbeater (Hellmayr, *ibid.*). The type locality was restricted to Río Frío, state of México, by Brodkorb (1944:401) on the basis that the type was collected by Bullock. According to Baird (1858:588), Wagler's specimen was the same as that used by Swainson for his description of *Garrulus sordidus* (see p. 415); Wagler acquired the specimen after Bullock's Museum of Mexican Curiosities was dispersed.

A fourth name, which has always resided in synonymy, is that of *Corvus azureus* Lichtenstein (1830). It was represented in the Berlin Museum in 1933 by two co-types collected by Deppe; according to van Rossem, these were the "large southern plateau race" [= *ultramarina*].

Subsequent to the description of the east Mexican races *couchii* and *potosina* (= *sordida*), no major change has occurred in the concept of the race *sieberii* or *ultramarina*, nomenclatural events notwithstanding.

Specimens examined.—Total, 99, divided as follows: (1) southern Hidalgo, 2; (2) Veracruz, Puebla, Morelos, and México, 42 (table 55); (3) Michoacán, 54 (table 56); (4) Jalisco, 1.

1) HIDALGO: Tulancingo, 2.

2) VERACRUZ: Cofre de Perote, 2; Jalapa, 8; Las Vigas, 2, and (at 8,000 ft.) 1; Mirador, 1; Mount Orizaba, 3; 5 mi. E Perote (8,700 ft.), 2. PUEBLA: 8 mi. NE Chalchicomula (10,350 ft.), 2; Mount Orizaba, 8; Río Frío Valley, 2. MORELOS: Huitzilac, 8; Tetela del Volcán, 2. MÉXICO: N slope, Volcán de Toluca, 1.

3) MICHOACÁN: Cerro de Tanicítaro (including Mount Tanicítaro, Tanicítaro, and 2–3 mi. N Apo-Rancho Escondido), 17; Cerro de San Andrés (20 mi. SSW Morelia, 9,000 ft.), 3; El Temazcal (20 mi. E Morelia), 3; 2 mi. E Los Reyes, 1; 15 mi. ESE Morelia, 1; Patambán, 4; Pátzcuaro, 4; 5 mi. S Pátzcuaro, 3; Nahuatztín, 1; Quiroga (N side Lake Pátzcuaro, 6,800 ft.), 2; San Gregorio (15 mi. S Pátzcuaro), 1; 1 mi. N San Juan (2,300 m.), 4; Uruampan (Los Conejos, 5,800 ft.), 3; Zacapu (6,000–10,400 ft.), 7.

4) JALISCO: Cerro García (32 mi. S Guadalajara), 1.

***Aphelocoma ultramarina colimae* Nelson**

Aphelocoma sieberi colimae Nelson (1899a:27), original description, part; Ridgway (1904:339, not of Nelson).

Aphelocoma sordida colimae, Hellmayr (1934:57), part.

Type.—Adult female, no. 156052, BS, USNM; Jacala, Jalisco; collected by E. W. Nelson and E. A. Goldman, March 6, 1897; orig. no. 3816 (Nelson, 1899a:27). Measurements of the type, which I have examined, are as follows (mm.): wing, 169; tail, 153; bill length, 17.1; bill depth, 10.1; tarsus, 40.6.

Nomenclatural history.—No changes have occurred in the history of this race other than a restriction of range made by Ridgway (1904:339), who based his statements strictly on specimens available to him. His restriction is followed in this paper, because specimens from at least one part of the range attributed to *colimae* by Nelson do not belong to that race.

Specimens examined.—Total, 55 (table 57). JALISCO: El Real Alto, 1; Hacienda San Marcos, Tonila, 2; Jacala, 2 (including type); La Ciénaga (7,000 ft.), 1; La Pisagua (9,000 ft.), 6; Los Masos (5,800 ft.), 11; Mascota (and La Laguna, NE Mascota, Sierra de Juanacatlán), 6; San Sebastián, 1; Sierra Nevada de Colima (including Volcán de Nieve, 9,000–13,000 ft., and Volcán de Colima, 10,000 ft.), 22; Sierra de Tapalpa (15 mi. W Sayula, 7,450 ft.), 1; 5 mi. SW Cocula (W slope Cerro Tecolote, 6,800 ft.), 2.

***Aphelocoma ultramarina* subsp.?**

Aphelocoma sieberi colimae Nelson (1899a:27), part.

Aphelocoma sordida colimae, Hellmayr (1934:57), part.

Specimens from interior Jalisco and adjacent Nayarit cannot be identified racially at this time. (For a discussion of their characters see p. 346.)

Although the range ascribed to *colimae* by Nelson (1899a) includes interior central Jalisco, there is no evidence that he had any specimens from that area. Presumably he based his statement of range in part on sight records. Hellmayr (1934:57) merely followed Nelson.

Specimens examined.—Total, 4. JALISCO: Tinguindi (ranch in municipality of Ixtlahuacán del Río, 15 mi. NNE Guadalajara), 2 (AM nos. 501127–8); 12 mi. W Yahualica (La Mesa de los Puercos, 8,000 ft.), 1. NAYARIT: 6 mi. S Ixtlán del Río (6,800 ft.), 1.

Aphelocoma unicolor

Nomenclatural history.—The existence of recognizable races of *A. unicolor* or of closely related "species" was first reported in 1903 with the naming of *coelestis* from Chiapas by Ridgway and *guerrerensis* by Nelson. Previously, *A. unicolor* was known from southwestern Mexico and Guatemala, the areas involved in the description of Ridgway's race from Chiapas and Guatemala. Judging by the criteria for recognition of species in vogue at the turn of the century, Ridgway must have regarded *A. unicolor* as a rather widely ranging species, since he described *coelestis* as a subspecies. He recognized, however, Nelson's "species" *guerrerensis*, which the latter reported from what was at that time a newly explored section of Mexico.

A. guerrerensis was reduced to a race of *A. unicolor* by van Rossem in 1928, when that investigator reported the existence of a fourth race, *A. u. griscomi*, at

the southern extreme of the geographic range of the species, a race which proved to be more similar to *guerrerensis* than to *unicolor* or *coelestis*. The nomenclatural changes proposed by van Rossem were of particular interest at the time of their publication because Oberholser (1919:136) had earlier adopted a subgeneric division of the known forms of *A. unicolor*.

On the basis of the fact that the tail is longer than the wing in *guerrerensis*, Oberholser (*ibid.*) placed that "species" in the subgenus *Aphelocoma*, whereas he placed the two then known races of *A. unicolor* in the subgenus *Sieberocitta* because in these the wing is longer than the tail. It may be noted that among the presently recognized races of *A. unicolor* the wing-tail ratio (based on means of those dimensions) ranges from 1.072:1 in *unicolor* to 0.975:1 in *guerrerensis*, whereas within the group of races and "species" placed by Oberholser in the subgenus *Aphelocoma* the wing-tail ratio ranges from 0.980:1 in *A. "californica"* (= *coerulescens sumichrasti*) to 0.806:1 in *A. "cyanea"* (= *coerulescens coerulescens*). Thus the mere fact of longer or shorter tail than wing, when emphasized through subgeneric categories, obscures the greater differences among the forms placed together by Oberholser in one subgenus. The striking variation in the wing-tail ratio of the *A. coerulescens* complex invalidates Oberholser's chief reason for maintaining the subgenera *Aphelocoma* and *Sieberocitta*.

Subsequent to van Rossem's (1928) brief review of the races of *A. unicolor*, one important change has occurred, namely, the transfer of the name *unicolor* to the race of Chiapas and Guatemala previously known as *coelestis*. This was necessitated by the discovery that Du Bus' type of *unicolor* was actually representative of Ridgway's *coelestis* (van Rossem, 1942a).

The remaining facts concerning nomenclatural history are adequately recorded in the synonymies which follow. It may be added that the name *Cyanocitta ultramarina* Sumichrast (1869:554), doubtfully placed in the synonymy of *A. u. "unicolor"* (= *concolor*) by Ridgway (1904:344), can be included there since the facts of differential altitudinal distribution reported by Sumichrast for that species and his "*Cyanocitta sordida*" have been confirmed by subsequent explorers. *C. sordida* is a synonym of *C. ultramarina*, and Sumichrast erroneously used the latter name for *A. u. concolor*.

***Aphelocoma unicolor unicolor* (Du Bus)**

Cyanocorax unicolor Du Bus (1847:108), original description.

Cyanocitta unicolor, Salvin (1866:194).

Aphelocoma unicolor, Sharpe (1877:118), part.

Aphelocoma unicolor coelestis Ridgway (1908:108).

Aphelocoma unicolor unicolor, van Rossem (1942a:212).

Type.—Specimen of unknown sex, Brussels Museum (van Rossem, 1942a:212); van Rossem's measurements of wing and tail, 172 and 165 mm., respectively; collected by Auguste Ghiesbreght, "probably in the spring of 1838 or 1839" (van Rossem, *ibid.*). Type locality restricted to Ciudad de las Casas (= San Cristóbal), Chiapas, by Brodtkorb (1944:402).

The type locality of Ridgway's *A. u. coelestis* is also San Cristóbal. The type is an adult male, no. 144685, USNM (Fish and Wildlife Service Collection); San Cristóbal; obtained by Nelson and Goldman, September 24, 1895; orig. no. 3106.

Measurements of the type, which I have examined, are as follows (mm.): wing, 167; tail, 157; bill length, 19.7; bill depth, 11.6; tarsus, 43.6.

Specimens examined.—Total, 45 (table 58). CHIAPAS: Barranca Honda (1,200 m., Distrito de Libertad), 1; Pico de Loro (2,200 m., Distrito de Mariscal), 3; Rodeo (Distrito de Mariscal), 1; San Cristóbal (= Ciudad de las Casas, type locality), 8; 9 mi. SE San Cristóbal, 1; Siltepec (Distrito de Mariscal), 1; Triunfo (2,000–2,020 m.), 2; Volcán Tacaná (including Aguacaliente; 2,200–2,800 m., Distrito Soconusco), 6.

GUATEMALA: Momostenango, 2; 8 mi. E Salamá, 2; San Agustín (Acazagustlán, Dept. Zacapa), 1; Sierra Santa Elena (9,480–10,000 ft., near Tecpán), 4; Tecpán, 9; Totonicapán, 1; unspecified, 3 (for localities, see Griscom, 1932:413).

***Aphelocoma unicolor oaxacae* Pitelka**

Cyanocorax unicolor, Du Bus (1848:pl. 17), part.

Aphelocoma unicolor unicolor, Hellmayr (1934:58), part.

Aphelocoma unicolor oaxacae Pitelka (1946a:44), original description.

Type.—Adult female, no. 39121, collection of Robert T. Moore, Pasadena, California; Moctum, Oaxaca, Mexico; collected by M. del Toro Avilés, October 18, 1941. The data on size and color are given on page 349.

Specimens examined.—Total, 3. OAXACA: Moctum, 1 (type); Mount Zempoaltepec, 1; Totontepec, 1.

***Aphelocoma unicolor concolor* (Cassin)**

Cyanocorax concolor Cassin (1848a:26), original description.

[*Cyanocitta*] *unicolor*, Bonaparte (1850:378).

Cyanocorax unicolor, Selater (1857:204).

Cyanocitta ultramarina (not *Corvus ultramarinus* Bonaparte), Sumichrast (1869:554; 1871:30).

[*Cyanurus*] *unicolor*, Gray (1870:5).

Aphelocoma unicolor, Sharpe (1877:118), part.

[*Garrulina*] *unicolor*, Heine and Reichenow (1882:117).

Aphelocoma unicolor unicolor, Ridgway (1904:344).

Aphelocoma unicolor concolor, van Rossem (1942a:212); Pitelka (1946a:44, not of van Rossem).

Type.—Specimen no. 3039, PAS [originally in the Rivoli (Massena) Collection]. "It is a molting bird with the following measurements: wing (not fully grown), 163 mm.; tail, 132; . . . tarsus, 40" (Brodkorb, 1944:402). My measurements of the type are as follows (mm.): wing, 159; tail, central feathers absent, measurement not taken; bill length, 19.3; bill depth, 10.3; tarsus, 39.6.

The type locality was fixed by Brodkorb (*ibid.*) as the eastern part of the state of México. Cassin (1848b:90) stated that *C. concolor* was obtained in Puebla, and it seems to me that a restricted type locality might best be selected in accordance with Cassin's early record.

Specimens examined.—Total, 17 (table 59). VERACRUZ: Córdoba, 1; Jalapa, 3; Jico (= Xico), 9; Mirador, 1; unspecified, collected by de Oca, 2; unspecified, 1 (type).

***Aphelocoma unicolor guerrerensis* Nelson**

Aphelocoma guerrerensis Nelson (1903:154), original description.

Aphelocoma unicolor guerrerensis, van Rossem (1928:362).

Type.—Adult male, no. 185539, BS, USNM; Omilteme, Guerrero; obtained by E. W. Nelson and E. A. Goldman, May 19, 1903; orig. no. 9926 (Nelson, 1903:154).

Measurements of the type, which I have examined, are as follows (mm.): wing, 166; tail, 171; bill length, 22.7; bill depth, 12.0; tarsus, 40.3.

Specimens examined.—Total, 85 (table 60). GUERRERO: Omilteme, 85 (including type).

***Aphelocoma unicolor griscomi* van Rossem**

Aphelocoma unicolor griscomi van Rossem (1928:362), original description, part.

Type.—"Male adult, no. 18181, collection of Donald R. Dickey [University of California at Los Angeles]; Los Esesmiles, Dept. Chalatenango, El Salvador; altitude 8,500 feet . . . ; February 4, 1927; . . . collected by A. J. van Rossem; orig. no. 11044" (van Rossem, 1928:362). Measurements of the type, which I have examined, are as follows (mm.): wing, 169; tail, 159; bill length, 21.0; bill depth, 10.8; tarsus, 43.7.

Specimens examined.—Total, 53 (table 61). EL SALVADOR (Dept. Chalatenango): Los Esesmiles (8,000–8,500 ft.), 12 (including type). HONDURAS: Alto Cantoral, 16; Cerro Santa María, 1; El Derrumbo, 3; Mount Pucea, near Gracias (6,600 ft.), 18; Rancho Quemado, 3. (For localities see Goodwin, 1942:108.)

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PLATES

PLATE 18

Variation in pattern among species of *Aphelocoma* and race groups of *A. coerulescens*. Specimens of adults in lateral view, top to bottom: *A. c. coerulescens* (AM 372063), *A. c. californica* (MVZ 72597), *A. c. nevadae* (MVZ 28084), *A. c. remota* (MCZ 163837), *A. ultramarina ultramarina* (BS 144364), *A. unicolor unicolor* (BS 144682).

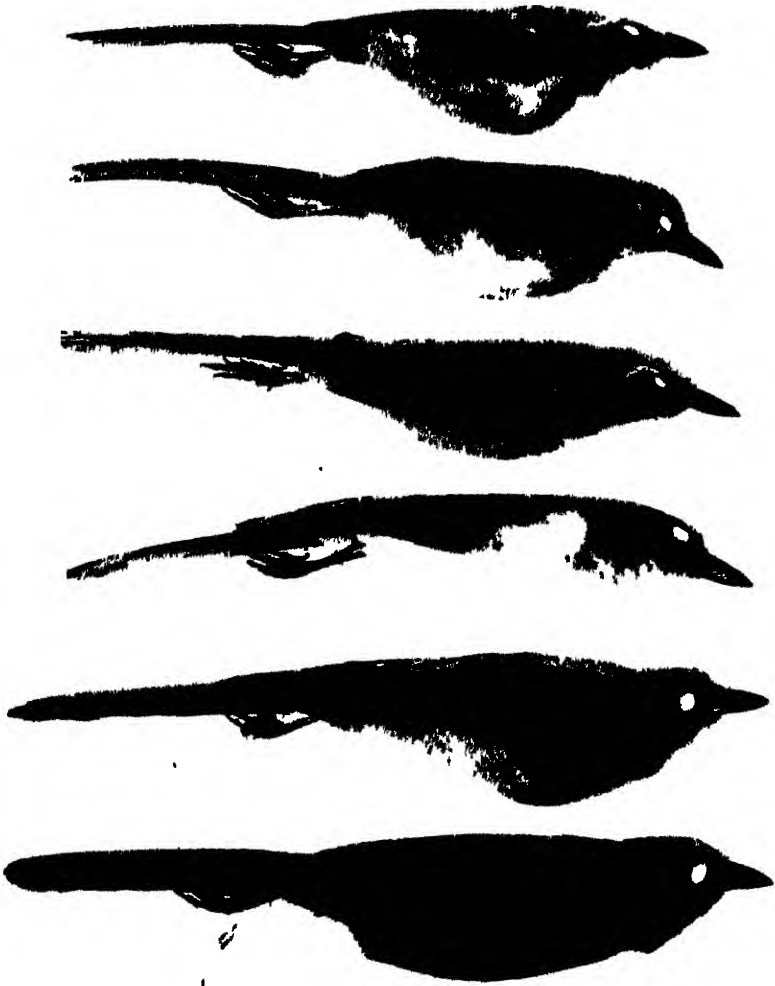


PLATE 19

Some of the specimens in ventral view

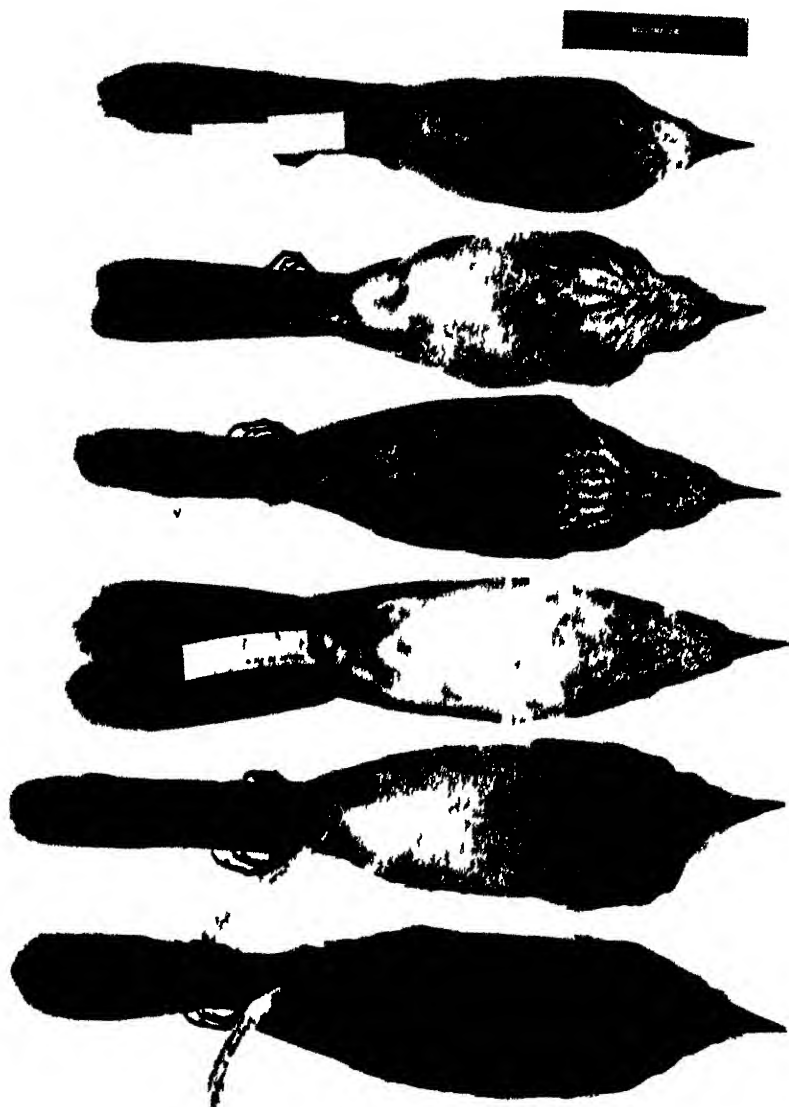


PLATE 20

Variation in pattern and intensity of dorsal coloration in genus *Iphlocoma*.
Specimens of adult males, top to bottom: *I. coerulescens coerulescens* (AM 57206), *I. c. insularis* (MVZ 5794), *I. c. californica* (MVZ 72597), *I. c. nevadae* (MVZ 28084), *I. c. sumichrasti* (US 144756), *I. ultramarina ultramarina* (US 144564), *I. unicolor unicolor* (US 144682), *I. unicolor quercusensis* (MCZ 172544).



PLATE 21

Ventral pattern of various races of *Aphelocoma coerulescens*. Specimens of males, top to bottom: *coerulescens* (MCZ 7206); *californica* (MVZ 72597); *woodhousei* (AM 72219); *leucana* (MCZ 51751); *cyanootis* (MCZ 98802); *sumichrasti* (BS 11176); *remota* (MVZ 95595). A specimen of *A. ultra marina scribda* (BS 111611) is added for comparison.

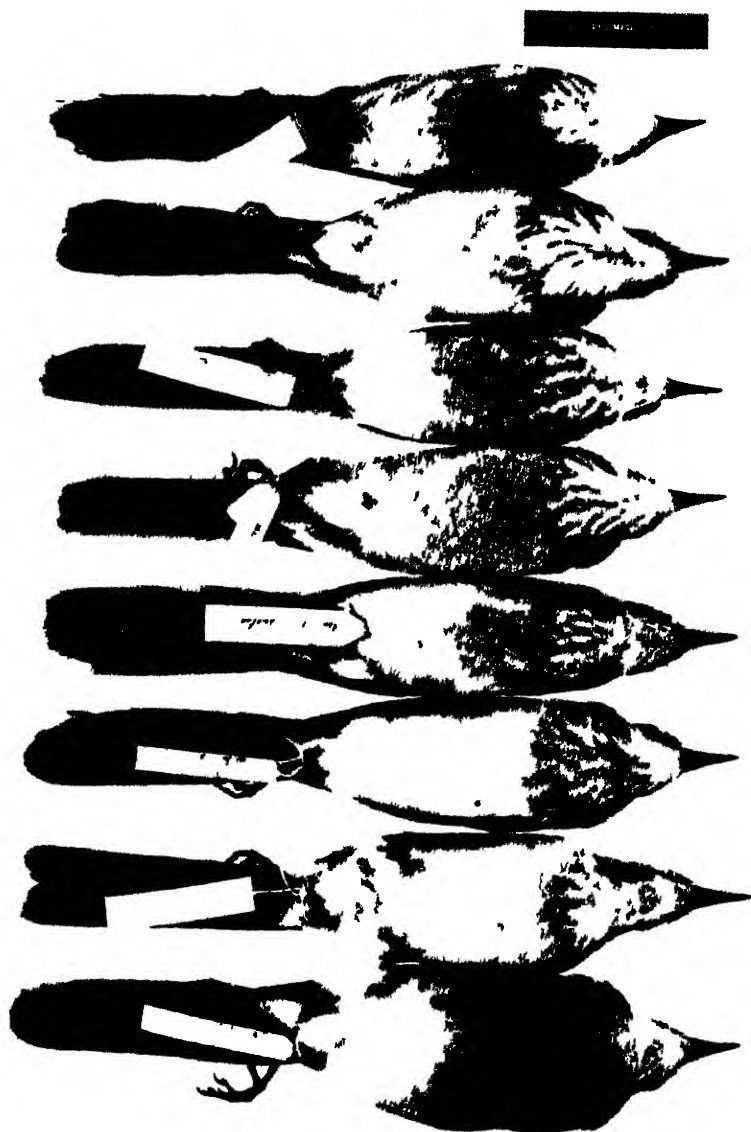


PLATE 22

Variation in size and form of bill in *Aphelocoma coerulescens* dorsal and lateral views. Specimens of adult males, top to bottom: *coerulescens* (AM 172061), *nevadae* (MVZ 28081), *remota* (MCZ 161837), *californica* (MVZ 72597), *insularis* (MVZ 31791)



PLATE 23

Pattern and intensity of ventral coloration in races of *Aphelocoma ultramarina*. Specimens of adult males, top to bottom: *couchii* (MCZ 320526), *sordida* (BS 144644), *ultramarina* (BS 144664), *gracilis* (BS 157239) *arizonae* (C M 142582)

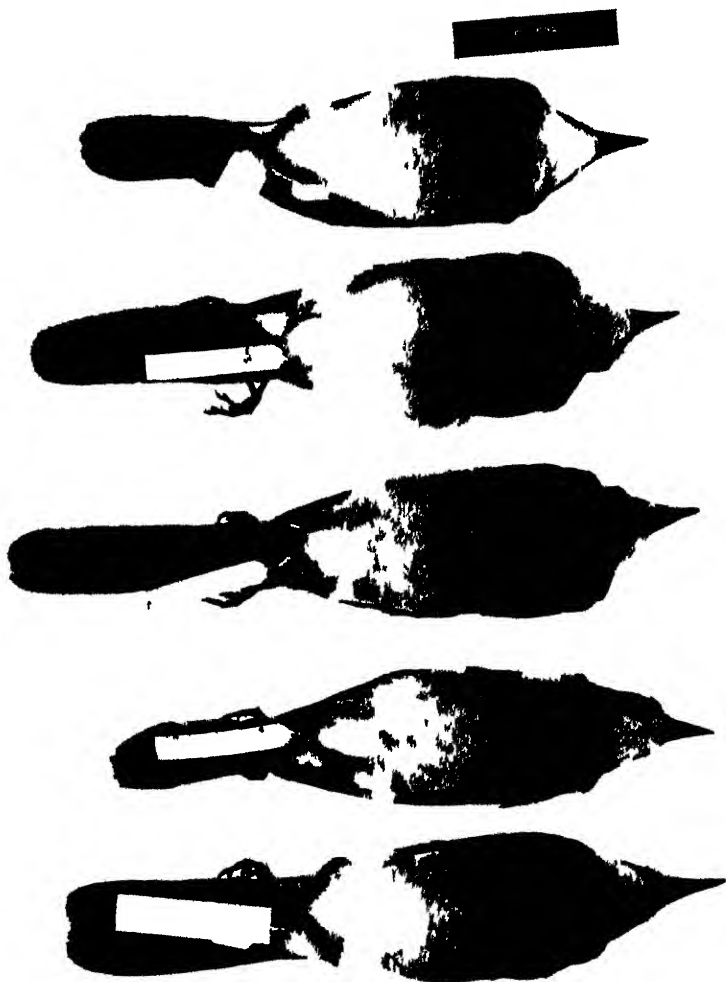


PLATE 24

Pattern and intensity of dorsal coloration in races of *Iphlocoma ultramarina*. Specimens as in pl. 23.

W. J. PITELKA

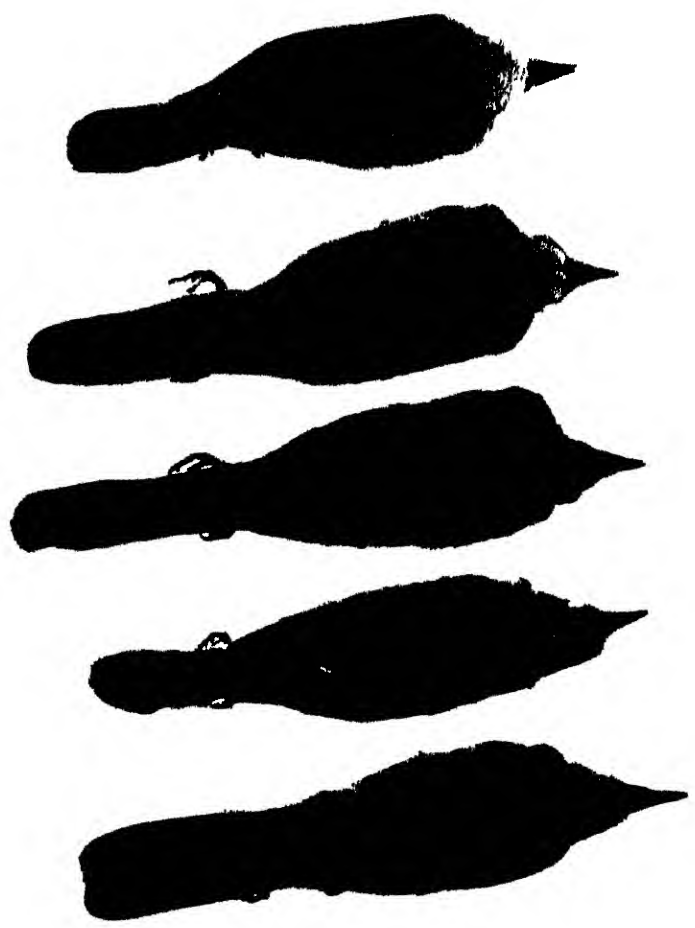


PLATE 25

Juvenil plumages in genus *Aphelocoma*. Specimens (top to bottom): 1. *A. californica* (MVZ 69663), 1. *A. neradai* (MVZ 81971), 1. *A. remota* (MCZ 163522), 1. *A. ultramarina arizonae* (MVZ 91105), 1. *A. unicolor quercensis* (BS 187517).

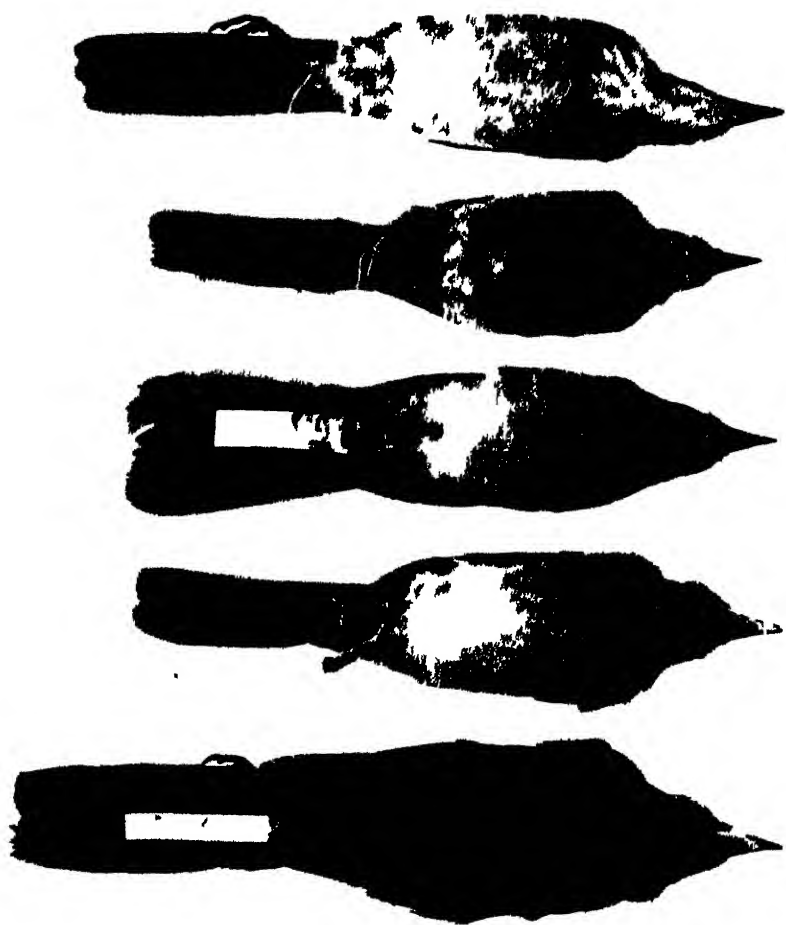


PLATE 26

a Islands of postclimax forest along Little Pine Creek at 6000 feet east slope of Sierra Nevada Inyo County California habitat of *Aphelocoma coerulescens superciliosa*. Tree species present *Quercus kelloggii* *Pinus ponderosa* *Salix lutea*. Common shrub species in adjacent sagebrush *Atriplex tridentata* *Ceanothus greggii* *Ephedra viridis* *Eriogonum fasciculatum*. Inyo Mountains in distance upper left corner inhabited by *A. c. nevadæ*.

b Broken secondary forest near Hayfork at 2400 feet Trinity County, California, habitat of *A. c. caurina*. Tree species present *Quercus garryana*, *Q. kelloggii* *Pinus ponderosa*. Common shrubs *Arctostaphylos manzanita*, *Ceanothus cuneatus*.



a



b

PLATE 27

a Pinon-juniper woodland along Montgomery Creek at 6900 feet west slope of White Mountains Mono County California habitat of *Aphelocoma occidens nevadae*. Trees typically 10-15 feet high. Common shrubs intermixed with them: *Artemisia tridentata*, *Larrea glandulosa*, *Chrysothamnus* spp., *Astragalus* sp.

b Oak-pine woodland near Beegum at 1650 feet western Tehama County California habitat of *L. californica*. Tree species present: *Quercus douglasii*, *Pinus sabiniana*. *Arctostaphylos manzanita* a shrub scattered among trees in more open parts of woodland is in foreground. Chaparral in distance dominated over large areas by *Adenostoma fasciculatum*.



a



b

PLATE 28

a Oak woodland and stream border oak woods east slope of Sierra Nevada at 5200 feet southwest of Olancha Inyo County California habitat of *Aphelocoma coerulescens superciliosa*. Oak present is *Quercus chrysolepis*. foreground sagebrush dominated by *Artemisia tridentata* *Chrysothamnus nauseosus* and *Lupinus arbustus*. Oak piñon woodland at higher elevations in distance Olancha Peak in distance at left.

b Upland vegetation west of Prisoners Harbor Santa Cruz Island California showing groves of scrub trees inhabited by *L. insularis*. Trees of similar form usually not exceeding 7 to 9 feet in height comprise woodland seen in distance of pl. 30a. Trees in left center foreground *Quercus wislizeni*. Photo by O. P. Peckham.



PLATE 29

Open forest of *Pinus remota* upper end of Christy Canyon Santa Cruz Island California habitat of *Aphelocoma coerulescens insularis* Photo by O. P. Folsom

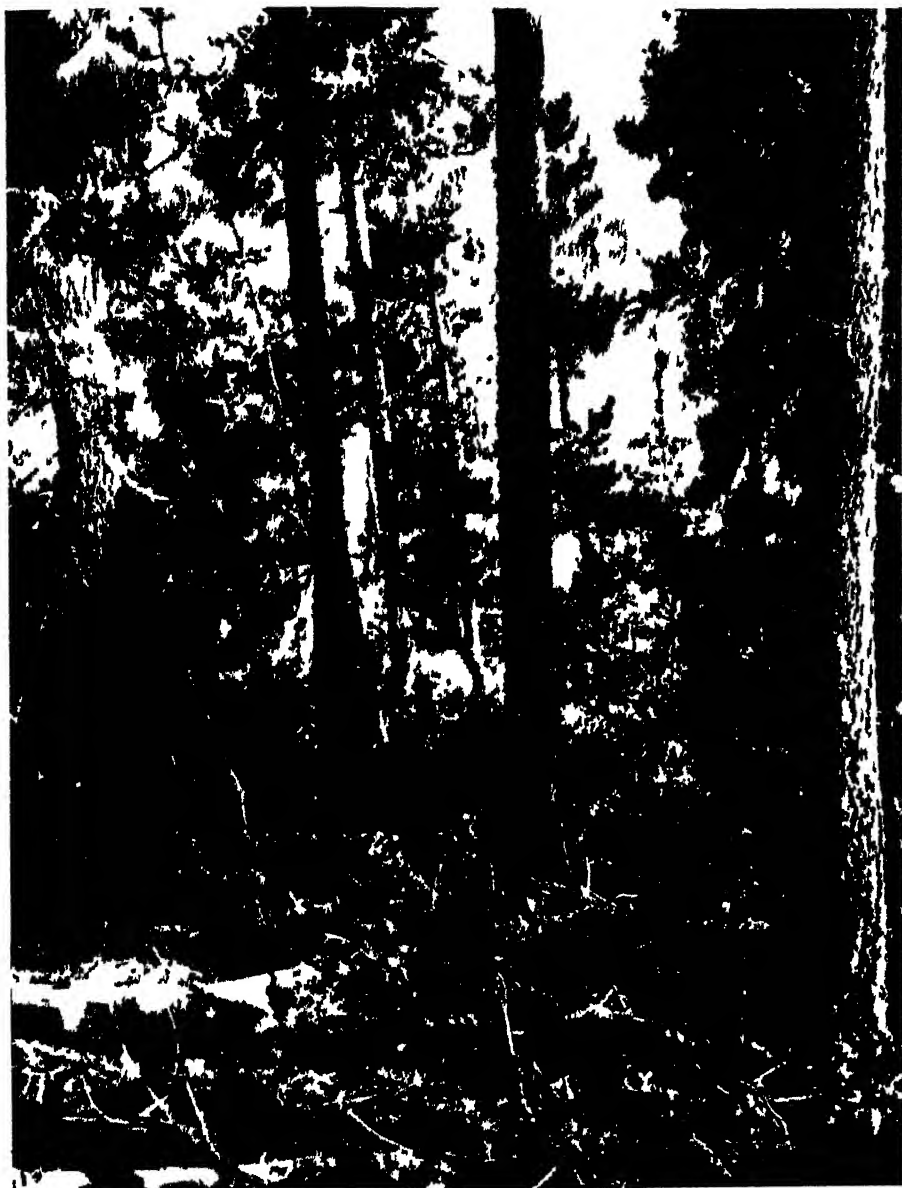


PLATE 30

General vegetation pattern widely prevalent in range of *Aphelocoma cyanilescens* on Pacific coast

a Scrub woodland (in distance) and groves of coast live oak *Quercus agrifolia* (foreground and left center) Puerto Canyon near Prisoners Harbor, Santa Cruz Island, California, habitat of *A. c. insularis*. Photo by C. P. Pearson

b Woodland and chaparral, southeast slope of Mount Diablo, Contra Costa County, California, habitat of *A. c. superciliosa*. Common shrubs of chaparral: *Adenostoma*, *Ceanothus cuneatus*, *Photinia*, *Arctostaphylos* spp. Common trees of woodland: *Quercus douglasii*, *Q. wislizeni*, *Aesculus californicus*, *Pinus sabiniana*



a



b

SUBSPECIFIC DIFFERENTIATION IN THE OLYMPIC SALAMANDER *RHYACOTRITON OLYMPICUS*

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BY

ROBERT C. STEBBINS AND CHARLES H. LOWE, JR.

(A contribution from the Museum of Vertebrate Zoology of the University of California)

THE AMBYSTOMID salamander *Rhyacotriton olympicus* (Gaige) ranges from middle Humboldt County, California (10.6 miles west of Dyerville), north into the Olympic Peninsula of Washington, west of the crest of the Cascade Mountains. There are few records for Oregon, where the species seems to be uncommon, but this apparent scarcity may be partly the result of inadequate collecting. The species is not yet recorded in northern Idaho and adjacent areas although it may occur there. This region is occupied by representatives of other amphibian species that are present in the humid coastal forests of the Pacific northwest: *Dicamptodon ensatus*, *Triturus granulosus* (recently found near Moscow, Idaho), *Plethodon idahoensis* (counterpart of *P. vandykei*), and *Ascaphus truei*. The ranges of *Ascaphus* and *Rhyacotriton* are almost identical along the coast.

From April 11 to 24, 1948, we intensively sought this salamander over the full length of its range. Nearly all animals obtained were brought to Berkeley alive. While under study they were kept in a dark room at 12°C for a period of nearly six months. Individuals were maintained in quart, glass-top fruit jars, two or three to a jar. A wet paper towel was placed in each container. The towel provided moisture, and its folds furnished places of retreat for the salamanders. The low, constant temperature and the inactivity of the animals made feeding unnecessary. There was nearly 100-per-cent survival at the end of the study, and all animals appeared in good condition when preserved.

From our material it was evident that there were two well-defined subspecies, which we here figure and describe.

Rhyacotriton olympicus olympicus (Gaige)

Ecnodion olympicus Gaige, 1917:2, original description.
Rhyacotriton olympicus, Dunn, 1920:56.

Range.—Principally, if not entirely, west of the crest of the Cascades in Washington from the Olympic Peninsula south to the Columbia River and probably coastally in Oregon to Cape Lookout, Tillamook County. In the north, ranges interiorly at least to Tacoma, Pierce County, and in the south to Oak Point, Cowlitz County, Washington.

Animals from Skamania and eastern Cowlitz and Lewis counties on the west slope of the southern Cascades of Washington are considered intergrades with *variegatus*.

Diagnosis of adults.—Above, uniformly dark chocolate brown with numerous fine whitish guanophores; dark dorsal pigmentation ends abruptly along sides; extensive suffusion of fine speckling of whitish guanophores along sides; below, un-

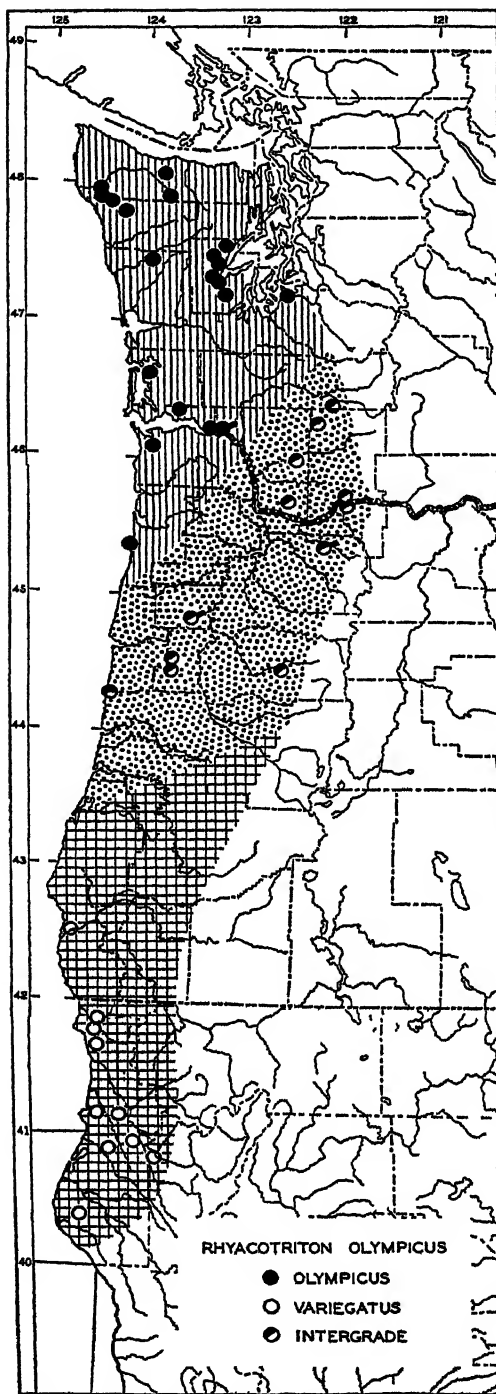


Fig. 1. Distribution of *Rhyacotriton olympicus*, showing ranges of subspecies and area of intergradation. Symbols with the appended bar show localities reported in the literature.

marked orange yellow or with mottlings of brownish in gular area and a few well-defined dark spots or blotches on underside of body and tail; some individuals have dark markings only in gular area.

General description (colors in life).—Adult generally dark chocolate brown above (Prout's Brown,* Mummy Brown, Raw Umber, and between Verona Brown and Bister), commonly grading to Cinnamon-Brown on head from behind eyes to tip of snout; eyelids olivaceous (Brownish Olive, Deep Grayish Olive, Saccardo's Umber, Medal Bronze, or Orange-Citrine); ground color usually lighter on tail and limbs, near Antique Brown; dorsal coloration of head and body uniformly brown, unspotted; limbs, tail, and lower sides, at margin of dorsal pigmentation, however, with variable number of dark mottlings, which may occur as rather definite spots; underlying color of limbs dull yellowish orange, largely obscured by dark mottlings; orange color (close to Mars Yellow) most apparent on inner toes and on upper surfaces of bases of limbs; dark dorsal pigmentation extends on sides to line connecting limbs at juncture of their ventral surfaces with body; margin of this melanic pigmentation irregular and accented by dark globs of blackish brown; below, rather uniformly orange yellow (dull Cadmium Yellow, Aniline Yellow, and between Light Cadmium and Aniline Yellow) darkening somewhat in area over liver to near olivaceous yellow (dull Sulphine Yellow) and commonly lightening on feet and anterior half of gular area to near Antimony Yellow; ventral color lightens on outer portions of lobes of vent in males to Apricot Yellow or Maize Yellow; gular area commonly with dark mottlings and scattering of dark melanic spots and blotches posteriorly on body; guanophores of skin widely distributed: in sensory pits of lateral line system and independently of pits; guanophores white, not branched or but slightly so, those of pit organs largest, widely spaced in several longitudinal rows on body: the dorsal, lateral, and ventral rows of lateral line organs; sensory pits in head region similarly marked; generally smaller, duller, more closely set guanophores form stippling in intervening areas between pits, being most abundant laterally where they form hoary suffusion between limbs and on sides of head and neck; on tail, guanophores most abundant basally, becoming rapidly fewer distally; moderate scattering of guanophores present dorsally and few ventrally; ventrally, most abundant in gular area; guanophores present in moderate numbers on dorsal surfaces of limbs but scarce ventrally; metallic, light-colored markings on blackish-brown iris, usually in about equal amounts in upper and lower portions; tendency toward light-colored pupillary line above and below pupil; metallic iridic pigment flecks may be stellate, may occur as blotches, spots, or lines; these flecks occur in various shapes and sizes and may be connected variously, sometimes in rather extensive reticulum; iridic colors recorded under magnification and with artificial light were: white, silver, gold, and buff (Cream Color, Maize Yellow, Baryta Yellow, and Orange Pink); several different colors sometimes observed in same eye, probably due in part to varying incidence of light.

DISCUSSION

Melanic pigmentation.—Under magnification the dark-brown areas of the skin are observed to be heavily melanic. This pigment seems to occur both within chromatophores and free near the surface of the skin. Melanophores occur at two levels. A

* Capitalized names of colors are from Ridgway, 1912.

deep layer of these cells forms a heavy network about the blood vessels and glands. The vessels appear margined with black. Branches of the melanophores extend toward the openings of the dermal glands, the positions of which are marked by their small, round, light-colored openings. These stand out against the brownish ground color. The ducts of the glands are surrounded by a dark ring of pigment, peripheral to which is a concentric lighter zone that overlies the body of the gland; the periphery of the glandular mass in turn appears darkly pigmented, which pigment merges with that surrounding the dermal vessels.

Overlying the deeper melanic layer are scattered, more widely spaced, stellate and punctostellate epidermal melanophores. Associated with them are numerous granules of melanin. These particles may in part be within invisible, highly branched processes of the superficial melanophores. However, their occurrence far removed from concentrations of pigment, presumed to be present in the reservoirs of the pigment cells, combined with a certain regularity in spacing of the particles, suggests that some of this pigment is outside the melanophores.

The deeper melanic layer tends to weaken or break up on the eyelids, limbs, and tail. This is most pronounced dorsally and distally on the sides of the tail. In these zones the only melanic pigment may be that of the superficial layers of the skin.

Melanophores form mottlings in the gular area of nearly all individuals. Occasional animals have the throat almost completely covered with dark blotches, whereas a few may lack gular markings entirely. Most animals have a scattering of dark spots and blotches on the ventral surface of the body and tail, but again there is variation from complete absence of markings to individuals with fourteen (and probably sometimes more) blotches posterior to the margin of the gular fold. The body blotches show no regularity of arrangement, occurring erratically anywhere from the gular fold to the tip of the tail.

Intraracial differentiation exists in the melanic pigmentation of *olympicus* on the east and west sides of the Olympic Peninsula. Thirty-four transformed individuals from the vicinity of Fischer's Ranch, Hoh River, Washington, on the west side of the Peninsula, obtained on September 20, 1919, were compared with a similar group of twenty specimens collected September 8, 1923, at Lake Cushman, Mason County, on the east side of the Peninsula (CAS specimens).

The animals from the west side were generally lighter, with dark spots along the sides of the body at the edge of the melanic pigmentation and on the tail. The caudal spotting was considerably more conspicuous, possibly because of the lighter ground color, than in animals from Lake Cushman. Tail markings in the Lake Cushman animals tended to be more numerous and diffuse and better characterized as mottlings rather than spots. Spotting of the sides was distinctly less pronounced in the Lake Cushman animals.

There was similarity in the character of the ventral markings, but again the Lake Cushman animals tended to average somewhat greater in melanic pigmentation. This is shown by the number of dark spots on the body, posterior to the gular fold. Spots associated with the lateral margin of the melanic pigmentation of the upper surfaces of the body are not included (table 1).

The spots in animals from Lake Cushman also appear to average somewhat larger and heavier, and they tend more to unite. This follows a similar tendency in

the gular area for the spots to join and to be more extensive and deeper in color. An adult female (CAS 64752) from Lake Cushman has the gular area completely covered with close dark mottling.

Other recently collected material from the two sides of the Peninsula bear out the preceding observations; hence the differences cannot be ascribed to time of collection or manner of preservation. Since these salamanders can change the general tone of their coloration, population differences in depth of ground color and features of pattern influenced thereby cannot be decided from examination of a few individuals. Thus an individual from Lake Cushman changed from near Dresden Brown to near Prout's Brown and remained in the light phase for several months while she was kept in a dark room at 12°C.

Other locally differentiated populations may exist. A high percentage of individuals from the north side of the Columbia River near Cathlamet, Wahkiakum

TABLE 1
VENTRAL MELANIC SPOTTING IN *Rhyacotriton olympicus olympicus*

Number of spots.....	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Number of individuals															
Fischer's Ranch.....	5	8	7	4	4	2	3	1							
Lake Cushman.....	1	3	7	3	3	4	2	3	1	1	1	2	0	2	1

County, lack or have very weak ventral melanophore development. Of four adults, two lack melanophores, one has one, and another five small melanic markings. Of the eight larvae from this locality, spotting is as follows: three unspotted and the remainder with 2, 3, 6, 10, and 12 spots. Similarly an adult and two larvae from six miles southwest of South Bend, Pacific County, on the coast, are immaculate. A single larva, however, has a few spots. Animals from localities not now represented are needed for a thorough analysis of such infraracial differentiation.

Peritoneal melanophores.—Melanophores are present in the lining of the body cavity in both the Hoh River and Lake Cushman animals. These cells are punctate or punctostellate in the dorsal mesentery and become more nearly stellate in a longitudinal area to one side of its base; the stellate cells give way laterally, about on a level (interiorly) with the upper bases of the limbs, to punctate and punctostellate cells. These more laterally situated cells become fewer and scattered and finally disappear roughly at a level corresponding with the margin of the melanophores of the skin. The lining of the ventral portion of the body cavity is essentially without melanophores.

Melanophores may be present in the testicular covering, on that of the *vas deferens*, in the liver and spleen, but they seem to be absent from the lungs and most of the digestive tract (except as associated with mesenteries). In females the ovaries are largely without them, but some may be present in the peritoneal coverings of the oviducts.

Again the Hoh River animals seem to be less heavily melanic, nine of ten individuals having a spotty arrangement of the melanic color in the dorsal longitudi-

5/5* [4 larvae]; Deer Lake, Soleduck River Valley, Olympic Mountains (MVZ 2); near Sol Duc Falls (CPS 2); Lake Crescent, 4.9 mi. SE Fairholm, along U.S. Highway 101 (MVZ 6/6). *Cowlitz Co.*—At falls 1 mi. E Oak Point (Slater, 1938, CPS 1 larva). *Grays Harbor Co.*—Quinault (CAS 3 [2 larvae], MVZ 1/1); small streams crossing Ewell Creek Trail about 4 mi. S Quinault River (SNHM 1 larva); rocky tributary of Ziegler Creek about 4 mi. S Quinault River on Ewell Creek Trail (SNHM 1). *Jefferson Co.*—Along Hoh River at following localities: vicinity of Fischer's Ranch (CAS 172 [70 larvae]); Hoh River (SCB 3 [2 larvae], USNM 1); Hoh River just below highway bridge (CPS 1); 9 mi. upstream from where U.S. Highway 101 crosses Hoh River (MCZ 2); along Hoh River Road, 7.4 mi. (MVZ 3/3 [1 larva]) and 4 mi. (MVZ 4/4 [2 larvae]) ESE junction with U.S. Highway 101; Jackson Ranger Station (MVZ 4); other localities: 1.5 mi. S Bogachiel, along U.S. Highway 101 (MVZ 1/1 larva); near Spruce (Slevin, 1928). *Mason Co.*—Lake Cushman (CAS 20, UMMZ 4, AMNH 48 [47 small larvae], SCB 2, USNM 1, MCZ 1); following places in vicinity of Lake Cushman: Big Log (AMNH 29 [6 larvae]); Mount Rose (AMNH 9 [4 larvae], MCZ 2 [1 larva], UMMZ 41 [3 larvae], MVZ 2); creek on Mount Rose (UMMZ 4 [2 larvae], MCZ 2; UMMZ 5 [1 larva]); Mount Cushman (AMNH 4); Laundry Creek UMMZ 4, AMNH 1, CM 1, MCZ 2 [1 larva]; Antler Creek (UMMZ 3); Mount Ellinor (UMMZ 1 larva); Ellinor Creek (UMMZ 1 larva); McTaggart Creek (UMMZ 1); Staircase Camp (AMNH 22 [15 larvae], MVZ 4); 3 mi. N Staircase Camp, Skokomish River, 5 mi. upstream from present Lake Cushman (MVZ 4); Lake Cushman, 5 mi. N intake (CPS 3); Olympic Mountains (AMNH 1); Donahue Creek, Olympic Mountains (AMNH 2 larvae); Olympic Hot Springs (AMNH 2 [1 larva]); Skokomish River Valley (AMNH 1 larva); Madeline Creek (AMNH 1) and Pebleford Creek (AMNH 10 larvae) Skokomish River; Dry Creek (AMNH 3 larvae); Triple Trip Creek (AMNH 13 [5 larvae]); Elk Creek (AMNH 1); Hoodspout (AMNH 221); 6 mi. N (SCB 1 larva) and 7 mi. N Shelton (SCB 1); Government Camp beyond Shelton (CPS 4 larvae); Jefferson Creek on Hamma Hamma River (CPS 1). *Pacific Co.*—Falls 6 mi. SW South Bend (CPS 4 [3 larvae]). *Pierce Co.*—Tacoma (SCB 1). *Wahkiakum Co.*—8 mi. (MVZ 9/9 [6 larvae]) and 6.3 mi. (MVZ 3/3 [2 larvae]) SE Cathlamet, along U.S. Highway 830; small stream 3 mi. E Grays River (village in W part Wahkiakum Co.) (Slater, 1933); at a falls on highway 1.7 mi. W Wahkiakum-Cowlitz co. line (Slater, 1933).

***Rhyacotriton olympicus variegatus* subsp. nov.**

Type.—Adult female, MVZ 45868, collected by Robert C. Stebbins November 16, 1947, 1.3 miles west of Burnt Ranch Post Office, Trinity County, California.

Range.—Coast area in northwestern California and southwestern Oregon, from southern Humboldt County, California, north to the Rogue River Valley, Curry County, Oregon. Ranges inland in California to the vicinity of Willow Creek, in extreme western Trinity County.

Animals from the central coast of Oregon and interiorly to the north, although similar to *variegatus*, are considered intergrades with *olympicus* (p. 474). The identity of the population of the Rogue River is somewhat uncertain. It is included with *variegatus* on the basis of the examination of two adults and two larvae (preserved) and Fitch's (1936:637) reference to the ventral coloration (in life) of his material as "... bright lemon yellow ... with scattered black dots." Fitch's specimens were five young, the three smallest with stumpy external gills.

Diagnosis of adults.—Above, with olive or pale olive ground color largely obscured by numerous spots, blotches, and reticulations of black to blackish brown; white speckling (guanophores), although present, usually not as conspicuous as in *olympicus*, probably because of broken, lighter-colored background; dark markings along sides grade into similar markings of venter; whitish guanistic speckling of sides not conspicuous; below, generally greenish yellow commonly heavily flecked and spotted with dark melanic blotches of variable size; dark markings seldom concentrated in gular area; gular area commonly marked like remaining underparts.

* The figure above the line is the total number of individuals examined; that below, those seen alive.

General description (colors in life).—Adult above, generally pale olive (between Buffy Olive and Olive, between Buffy Olive and Citrine Drab, Olive Lake, or Light Brownish Olive) in ground color, darkened by numerous blotches and reticulations of black or blackish brown; general aspect of dorsal coloration lighter than *olympicus*; snout similar in color to that of *olympicus* (Mikado Brown); eyelids olivaceous; ground color somewhat lighter on tail and limbs, with variegations as on body; dark blotches tend to form pair of longitudinal streaks on either side of upper base of tail that may set off nearly clear area of ground color; dark markings on body tend to become better defined on lower sides, perhaps partly owing to lightening of ground color; upper bases of limbs and upper surfaces of inner toes tend to be yellowish (Yellow Ocher) owing to less melanic obscuring of ground color; no sharp line between dorsal and ventral coloration along sides as in *olympicus*; dorsal mottling grades into ventral blotching; below, generally greenish yellow (Olive-Ocher to Deep Colonial Buff; slightly lighter than Pyrite Yellow; Yellow Ocher; Olive-Ocher to Yellow Ocher; or slightly more yellowish than Sulphine Yellow) grading to more orange yellow (between Cadmium Yellow and Light Cadmium; Apricot Yellow to Buff Yellow; between Citrine Yellow and Wax Yellow) on vent lobes of males; ventral color lightens in anterior gular area; commonly with considerable numbers of dark spots and blotches of irregular outline, highly variable size, and of irregular distribution over all ventral surfaces except for narrow area on underside of tail, where markings usually scarce; guanophores of skin similar in form, color, and distribution to those of *olympicus* but less conspicuous due to lighter ground color and variegated pattern; light pigment of iris similar to that of *olympicus*.

DISCUSSION

Melanic pigmentation.—*Variegatus* is similar to *olympicus* in having both deep and superficial dermal melanophores and a dispersion of fine melanic dermal pigment granules that appear to lie outside the melanophores. It differs from the northern subspecies principally in its extensive reduction of the melanophores of the deeper-pigmented zone of the skin.

There are extensive breaks in the distribution of these cells, resulting in a scattering of irregularly outlined, variously connected or isolated dark blotches. These blotches exhibit no regular arrangement. There is a tendency, however, for blotching to be absent in the vicinity of the guanistically pigmented pit organs, with the result that some individuals possess a row of widely spaced, longitudinally arranged light areas on either side of the midline, from the neck to the sacral region. These light areas, each with a guanistic pit organ in its center, may or may not be paired across the body. Such light areas do not appear in adult *olympicus*.

Blotches on the sides tend less often to be connected than dorsally on the body. They generally appear more intensely black, perhaps because of the lighter background color. Limbs and eyelids are marked like the body.

In ventral markings there is a greater difference between the coloration of the gular area and body in *olympicus* than in *variegatus*. Blotches on the body tend to be larger and less numerous in the former and to be more evenly outlined. There seems to be a greater range in size of the spots of a single individual in the Cali-

fornia animals. The melanophores possess a similar relationship ventrally as they do dorsally, occurring at varying depths in the skin. This can be observed best in the gular area. The most superficial layer, however, seems more often to be reduced.

The mesenteries and peritoneal covering of the testes and oviducts are more often and more extensively covered with melanophores in animals from Lake Cushman than in those from California. On the other hand, these cells seem to extend farther toward the ventral midline in animals from Del Norte County. Internal melanophores are similarly distributed in the two groups, however.

Other characters, such as size, proportions, and counts of teeth, are discussed under the subspecies *olympicus*.

Locality records.—CALIFORNIA: *Del Norte Co.*—8 mi. NE Crescent City (CAS 4 [2 larvae]); Mill Creek Park (CAS 17 [1 larva]); small tributary near mouth Wilson Creek, about 7 mi. N Klamath River (MVZ 1). *Humboldt Co.*—N slope Indian Butte, in mountain torrent along U.S. Highway 299 (SNHM 3 larvae); 8 mi. N Klamath (CAS 1 larva); Boise Creek, 800 ft. \pm , about 2 mi. W Willow Creek P. O. (MVZ 1/1); 3.1 mi. E (MVZ 8/8 [3 larvae]), 3.6 mi. E (MVZ 2/2) and 5.5 mi. E Blue Lake, off U.S. Highway 299 (MVZ 1/1); 10.6 mi. W Dyerville (by road to Honeydew) (MVZ 4/4 [1 larva]); Maple Creek Spring, 3½ mi. NE Willow Creek, 2,700 ft. (MVZ); French Camp, 3,100 ft. (MVZ); Big Lagoon, 250 ft. (MVZ). *Trinity Co.*—1.3 mi. W Burnt Ranch P. O. (MVZ 7/7 [3 larvae]).

OREGON: *Curry Co.*—Ravine about 2 mi. W Lobster Creek, Rogue River Valley (SNHM 2 [1 larva]); Rogue River, 11 mi. above mouth (MVZ 2 [1 larva]).

INTERGRADATION

Area of intergradation.—The zone of intergradation seems to extend from the central coast of Oregon at Cape Perpetua, Lincoln County, diagonally northward across the Columbia River to the Cispus River north of Mount Saint Helens, Lewis County, Washington. Systematic treatment of animals from Oregon and the southeastern portion of the range of the species in Washington is provisional owing to the fact that decisions have been based (with the exception of animals from Perham Creek, Hood River County, Oregon) on preserved specimens. We have made our determinations solely on the distribution and arrangement of the melanic pigments. To what extent the trend in lipid coloration follows that of the melanic pigmentation remains to be seen from the study of living animals. Animals from Perham Creek, Oregon, were found to be intermediate in the coloration of the ventral surfaces between the yellow orange of *olympicus* and the greenish yellow of *variegatus* when large numbers of individuals from the three areas were compared simultaneously.

Description of representative adult.—Specimen from Perham Creek, Wygant State Park, Hood River County, Oregon (color in life). Ground color above between Buffy Brown and Olive-Brown grading on head from behind eyes onto snout to Hazel; eyelids Clove Brown; numerous small dark spots and blotches scattered over all dorsal surfaces, generally somewhat finer than in typical *variegatus*; ground color of limbs above close to Old Gold with upper bases of limbs near Chamois; ventral color between Aniline Yellow and Sulphine Yellow (former on underside of tail, limbs, and in gular area, and latter on anterior half of abdomen and chest); guanophores of skin and iris not notably different from *variegatus* and *olympicus*.

Melanic pigmentation.—Specimens from headwaters of Elk Creek, Mary's Peak,

Benton County, Oregon (OSCMNH nos. 387 ♀, 385 ♀, 386 ♂, 392 ♀). These individuals resemble animals from California except that the deep dorsal and ventral melanophores form generally smaller, more widely spaced blotches.

Storm Creek, Linn County, Oregon (OSCMNH no. 111 ♀). This locality lies interiorly to the Willamette Valley on the west slope of the Cascade Mountains. Living material from this locality may show the population represented by this individual to be indistinguishable from *variegatus*. The animal has heavy dorsal markings and moderately developed ventral blotching. It has been considered an intergrade because of the somewhat weaker ventral melanic pigment compared with the average condition in *variegatus* and because of its geographic position.

Alder Creek, 7 mi. above Sandy, Clackamas County, Oregon (Slater, 1938). Several specimens collected by M. Johnson and H. Richardson are referred to by Slater as "light brown with small black spots on their lateral and dorsal surfaces and . . . light cream colored on the ventral surface instead of the customary lemon-yellow. This last is likely a larval character."

Cispus River, 1 mi. W Iron Creek, Lewis County, Washington (OPS specimens). These animals have the largest blotches among representatives of the intergrading populations. They approach the uniform dorsal coloration of typical *olympicus* but at the same time in their mottled appearance show an affinity with animals to the south.

On February 2, 1949, we received from Dr. Robert Storm colored photographs of an adult female from central coastal Oregon. If we can rely on the colors, the animal was near *olympicus* in ventral pigmentation but perhaps somewhat less intense yellow orange (more a dull orange); the dorsal ground color also seemed nearest to this race. In pattern, however, it was like *variegatus*.

Locality records.—OREGON: Benton Co.—Mary's Peak (Graf, *et al.*, 1939); Elk Creek, Mary's Peak (OSCMNH 15 [7 larvae]); Alder Creek, tributary of Alsea River, 10 mi. SW Philomath (OSCMNH 2 [1 larva]). Clackamas Co.—Alder Creek, 7 mi. above Sandy (Slater, 1938). Hood River Co.—Oxbow Salmon Station, Cascade Locks (SNHM 21 [18 larvae]); Oxbow Springs, near Cascade Locks (from hatchery troughs) (SNHM 14 larvae); Porham Creek, Wygant State Park (MVZ 14/14 [11 larvae]). Lincoln Co.—Small tributary of Nash Lake (Graf, *et al.*, 1939); small tributaries of Fall Creek on W side Grass Mountain (Graf, *et al.*, 1939); Cape Perpetua, 3 mi. S Yachats (OSCMNH 3 [2 larvae]). Linn Co.—Storm Creek (OSCMNH 2 larvae); Middle Santiam River above Foster (Graf, *et al.*, 1939); ½ mi. E Crazy Creek, S Santiam Highway (OSCMNH 1 larva); Sheep Creek (♀) near South Santiam Highway (U.S. 20) (OSCMNH 1 larva ♀). Polk Co.—10 mi. above Hoskins on Luckiamute River (Graf, *et al.*, 1939).

WASHINGTON: Clark Co.—Camp Bonneville (Slater, 1938, OPS 6 larvae); Tum Tum Mountain, 1 mi. ± E (OPS 8 larvae). Cowlitz Co.—Yale (Slater, 1938) and 3 mi. E Yale (OPS 2 larvae). Lewis Co.—Cispus River 1 mi. W Iron Creek (OPS 3 [1 larva]). Skamania Co.—Spirit Lake (OPS 3); 2.6 mi. E Stevenson (OPS 1); Stevenson, about 2 mi. E (OPS 2 larvae).

LARVAE

Young larvae are much alike in dorsal melanic pigmentation throughout the range of the species, tending toward a mottled style of coloration similar to that of adult *variegatus*. Individuals of similar size were compared from localities near the extremes of the range: Blue Lake, Humboldt County, California, and Lake Cushman, Mason County, Washington. The most conspicuous difference between them lies in the tendency toward greater ventral spotting in the animals from California, a difference also present in the adults. As the larvae of *olympicus* approach meta-

morphosis, they lose their mottled appearance and become more uniformly colored like the adults. Although adult *olympicus* from the vicinity of Lake Cushman, on the east side of the Olympic Mountains, differ slightly in melanic coloration from those west of the mountains, we could find no such differences in their larvae.

Close inspection reveals that the deep melanic pigment of the skin is irregularly distributed, forming a more or less broken network. There are gaps at the sites of the pit organs of the lateral line system, and there is commonly a light, melanophore-free area basally on the dorsum of the tail. Melanic pigment is concentrated on either side of this light zone, margining it with black.

Very young larvae have nearly white venters, but with growth, lipid pigment becomes evident. Larger larvae approach the adults in ventral color. Those of *olympicus* tend toward orange; larval *variegatus* tend toward greenish yellow. Larvae from Perham Creek on the Columbia River, in a zone of intergradation, like the adults, are intermediate in ventral lipid coloration.

HABITAT

The microenvironment of *Rhyacotriton olympicus* appears uniform throughout the range of the species. It is possible to observe good numbers of these animals once the ecological niche is recognized. Whether in Washington, Oregon, or California, this niche is characteristically one of a cold, permanent stream with small, water-washed or moss-covered rocks (usually rock rubble) in and along the edges of running water. Often the main stream is a cascading one. Seeps and small, trickling, tributary streams with rocks of small dimension are sites at which numbers of these salamanders may be found. The rocks under which they rest are generally small and usually do not exceed diameters of five to six inches. The animals are less frequently found under moss and wood than under rocks.

Streams harboring *Rhyacotriton* usually have a good leaf canopy, especially during the summer months. Douglas fir, tanbark oak, bay, madrone, alder, and maple are common species along such streams; within the range of *variegatus* the coast redwood is another conspicuous component. Abundant understory vegetation, much moss, and a thick leaf mat are characteristic of the stream banks.

Rhyacotriton usually selects resting sites where the movement of the water tends to be relatively slow. They rest with their venters in shallow water, and one rarely finds an individual not in contact with either free water or at least a saturated substratum. Thus their body temperature tends to approximate that of the water, but due to the effect of evaporation from their moist skin surface, it is generally slightly lower than the temperature of the water. The animals are active at water temperatures between 5° and 10°C. At these temperatures individuals may escape with agility when they are exposed by turning their rock cover.

There is probably a difference in the environmental temperature met by *Rhyacotriton* in the northern and southern parts of its range, as suggested by the data presented in table 2. The close association of the adult animal with the water of its habitat (and the larvae are aquatic) probably imposes a constant and significant difference in the body temperatures of the two subspecies, that is, lower in the north (*olympicus*) and higher in the south (*variegatus*).

TABLE 2
TEMPERATURE RECORDS FOR ADULT *Rhyacotriton olympicus* FROM CALIFORNIA, OREGON, AND WASHINGTON*

Locality	Date	Time	Temperature, °C		
			Body	Water	Air
California					
Hennessy Creek, 1.3 mi. W Burnt Ranch P. O., along U.S. H'w'y. 299, Trinity Co.....	Apr. 23, 1948	6:00 P.M.	9.2	9.5	...
			9.3	9.5	...
	Nov. 19, 1948	5:30 P.M.	...	7.5	...
	Mar. 24, 1949	8:30 to	8.5	8.8	9.3
		9:00 A.M.	8.4	8.8	9.4
3.1 mi. E Blue Lake, along U.S. H'w'y. 299, Humboldt Co.....	Apr. 24, 1948	12:00 M.	9.6	9.6	9.9
			9.4	9.6	9.9
	Nov. 20, 1948	11:00 to 11:30 A.M.	7.5	7.7	7.1
			7.6	7.7	7.2
			7.6	7.7	7.2
	Mar. 23, 1949	3:00 P.M.	8.8	9.1	10.4
			8.9	9.1	10.7
10.6 mi. W Dyerville, along road to Honeydew, Humboldt Co.....	Apr. 24, 1948	1:30 to 2:00 P.M.	...	9.7	9.9
			...	10.9	10.0
	Nov. 21, 1948	9:00 to 9:15 A.M.	7.3	7.6	7.3
			7.5	7.6	7.2
			7.6	7.6	7.3
			7.4	7.6	7.3
Oregon					
Perham Creek, Wygant State Park, Hood River Co.....	Apr. 21, 1948	12:30 P.M.	7.9	8.0	12.0-12.2†
			7.8	8.0	12.0-12.2
			8.0	8.0	12.0-12.2
			8.0	8.0	12.0-12.2
Washington					
6.3 mi. SE Cathlamet, along U.S. H'w'y. 30, Wahkiakum Co.....	Apr. 11, 1948	6:30 P.M.	6.8	7.0	6.1
			...	8.0	7.2
8 mi. SE Cathlamet, along U.S. H'w'y. 30, Wahkiakum Co.....	Apr. 11, 1948		...	8.0	7.2
Quinalt, Grays Harbor Co.....	Apr. 12, 1948	4:00 P.M.	...	7.8	...
Hoh River (tributary stream), 4 mi. ESE junction U.S. H'w'y. 101, Jefferson Co.....	Apr. 13, 1948	12:00 M.	...	7.4	...
Lake Crescent, 4.9 mi. SE Fairholm, along U.S. H'w'y. 101, Clallam Co.....	Apr. 13, 1948	4:00 P.M.	5.8	5.9	6.6
			5.9	5.9	6.7
			5.9	5.9	6.6
			6.0	5.9	6.6
South end Lake Cushman, Mason Co.....	Apr. 17, 1948	4:30 P.M.	7.6	...	8.6

* Body temperatures are cloacal. Water and air temperatures were recorded at the site of capture unless otherwise noted. Air temperatures were taken above and within six inches of the animal except where stated otherwise.
† Air temperature not taken directly at site of capture of salamander.

REPRODUCTION

Mr. Phillips G. Putnam, on June 5, 1930, found *Rhyacotriton* apparently paired in one of the small streams near Lake Cushman, Washington. At least individuals of opposite sex were found together, and the ovaries and testes appeared to be in breeding condition. On June 7, in Elk Creek, a single egg was found attached to a tendril on the underside of a stone, and it was assumed to have been laid by *Rhyacotriton*. Another pair was found together on June 11 in Triple Trip Creek, where the water temperature was 10°C and the air temperature 14°C. Paired individuals were found in Madeline Creek on June 24 and on July 6, and after considerable search on the latter date a single egg was found, again assumed to have been laid by *Rhyacotriton*. Dissection of gravid females had led Putnam to conclude that a single individual must lay very few eggs, and he writes: "The *Rhyacotriton* eggs are apparently deposited singly beneath stones and are without conspicuous gelatinous capsules. An adult *Rhyacotriton* deposits approximately only twelve eggs which are naturally difficult to find" (Noble and Richards, 1932:19).

Seventeen adult females examined by us from California to Washington, obtained at different times of the year, averaged 9.2 ova (range 7 to 15) per female. Counts were made only in individuals possessing ova 2 mm. or more in diameter. The largest eggs were found in a female 55.8 mm. in snout-vent length, collected April 13, 1948, near Forks on the Calawah River, Clallam County, Washington. They measured 3.9 mm. In our material from Washington, large ova were found in females in middle April through early July, suggesting a spring or early-summer laying period. Ovarian eggs were generally considerably smaller in individuals taken in August and November. Several of these fall-taken individuals possessed large eggs, however. Two adult females obtained on October 1, 1932, possessed respectively 7 and 10 ovarian eggs about 3.4 mm. in diameter. Increase in diameter of the oviducts was correlated with increase in size of ova. Animals obtained in California suggest that oviposition may occur earlier in the southern part of the range. Five females collected in mid-February possessed ovarian eggs approximately 3 mm. in diameter.

Noble and Richards (1932:20) induced females to lay by means of pituitary implants. The eggs were attached to the sides and upper surfaces of the rocks placed in their containers. The average number laid by five females was 5, the maximum 8 and the minimum 3.

Eggs.—The eggs are large and pigmentless. In formalin they average 4.5 mm. exclusive of the capsules. In the living egg there appear to be three capsules: a soft, gelatinous inner one, a firmer, more opaque middle one, and a thick, transparent outer capsule. In the fresh egg the middle capsule was so thin that it might be considered merely a membrane covering the inner capsule. In the preserved egg the middle capsule is very distinct. For a few hours after laying, the outer capsule exhibited a series of fine ridges. By the time the two-cell stage was reached, these ridges had entirely disappeared. (Noble and Richards, 1932:20.)

Males from Washington largely lacked spermatozoa in the sperm ducts in Sep-

tember. Several taken in mid-April and in early July had ducts well laden with sperm. Four adult males obtained in mid-February, 1942, in California and a single one found on November 16, 1947, had the sperm ducts filled with spermatozoa.

SUMMARY

Two subspecies of *Rhyacotriton olympicus* are described, *olympicus* and *variegatus*. *Olympicus* of Washington and northwestern Oregon is chocolate brown above, yellowish orange below, and is speckled with white guanophores, most conspicuously along the sides of the body. *Variegatus* of California is dull grayish olive above with numerous dark-brown or blackish spots, blotches, and reticulations; the venter is yellow or greenish yellow with rather widely distributed scattered black spots, not notably concentrated in the gular area; guanophores are present but less conspicuous than in *olympicus*.

The largest animals occur in the vicinity of Lake Cushman on the east side of the Olympic Peninsula. In other parts of the range of the species, size appears to be nearly uniform. *Olympicus* has a shorter snout and smaller eyes than *variegatus*, and the vomerine teeth are fewer and the rows are more sharply arched anteriorly. Aside from the vent lobes of adult males, we observe no significant external sexual differences.

Intergradation occurs over an extensive area, chiefly in Oregon. Additional living animals are required to characterize accurately the trends in characters and to properly delineate the zone of intergradation. On the basis of dorsal blotching alone, *variegatus* might be considered to extend to the Columbia River or even into parts of southern Washington.

The habitat is uniform throughout the range of the species, the animals frequenting cold (5.9° to 10.9°C , range of our records) permanent streams, where they are found under rocks and moss, usually in moving water. They seem to favor water trickling through moss-covered rock rubble rather than the deeper, stronger currents. Streams are typically well shaded with trees such as Douglas fir, tanbark oak, madrone, maple, and redwood present in various parts of the range. The adults were found in saturated situations or in the water.

Females contain 7 to 15 (average 9) eggs. Oviposition apparently occurs in spring and early summer, the eggs being attached to the undersides of stones and to moss in streams. Some fall laying, however, may occur, as suggested by large ova in two females from Washington obtained in October. The eggs are large (4.5 mm., Noble and Richards, 1932) and pigmentless, with apparently three jelly capsules.

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* Abbreviations used in locality lists.

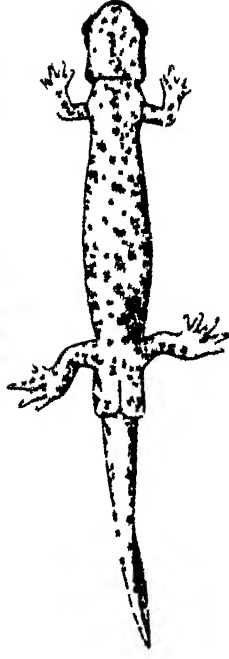
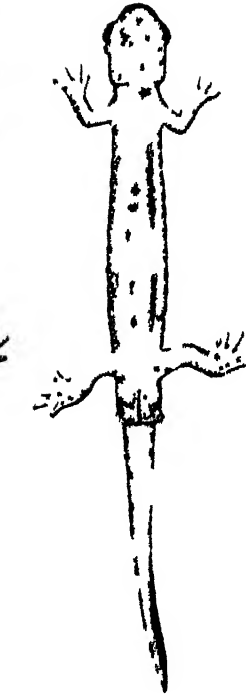
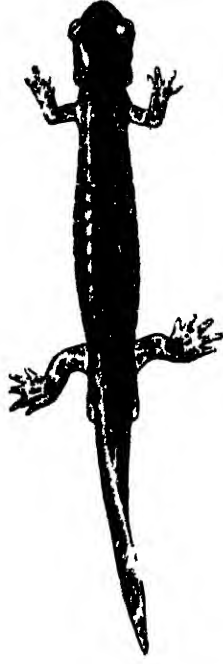
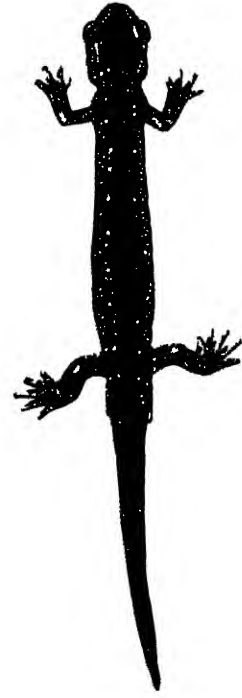
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PLATE

PLATE 31

Subspecies of *Ehyacotriton olympicus*, showing differences in coloration. *Olympicus*—Adult male from a stream at the south end of Lake Cushman, Mason County, Washington. *Variegatus*—Adult male from 13 miles west of Burnt Ranch Post Office, Trinity County, California.



A. Stebbins

20 mm

VARIEGATUS

OLYMPICUS

RHYACOTRITON OLYMPICUS

RELATIONSHIPS AMONG THE
GARTER SNAKES OF THE
THAMNOPHIS ELEGANS
RASSENKREIS

BY
WADE FOX

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RELATIONSHIPS AMONG THE GARTER SNAKES OF THE THAMNOPHIS ELEGANS RASSENKREIS

BY

WADE FOX

(A contribution from the Museum of Vertebrate Zoology of the University of California)

INTRODUCTION

IN THE COURSE of obtaining specimens of garter snakes of the genus *Thamnophis* for studies of the reproductive cycle, extensive collecting and field study were carried on in central California in 1946, 1947, and 1948. Examination of the specimens revealed the need for several taxonomic changes within the species *Thamnophis elegans*. This led to a reëxamination of all races of the species and to certain new interpretations of their interrelationships.

The present concepts of the taxonomy of Pacific coast garter snakes are based for the most part on the monographic revisions of Fitch (1940 and 1941). In 1940 Fitch reviewed the garter snakes of the Pacific coast and showed that, with the exception of *Thamnophis sirtalis*, they were closely related species and subspecies of the "*ordinoides* artenkreis." He divided this complex into three natural groups—Elegans, Hydrophila, and Ordinoïdes—on the basis of morphology and ecology. His Elegans group included the intergrading subspecies *T. ordinoides elegans*, *T. o. vagrans*, *T. o. biscutatus*, and *T. o. hueyi*. He regarded these forms as being more or less generalized as to ecology and unspecialized as to morphology. Fitch (1940:48) characterized the group as follows:

... 8 pairs of supralabials and 10 pairs of infralabials; not fewer than 21 scale rows (except rarely in *elegans*); a broad flat head; a blunt muzzle with the internasals broadly in contact with the rostral, their combined contacts exceeding the contact of either nasal with rostral; swollen posterior supralabials covering large salivary glands; a distinct yellow dorsal stripe extending the full length of the body; relatively small eyes; dark, heavily pigmented iris; large pupil; and no red in the coloration.

He found that *biscutatus* is primarily aquatic, that *elegans* and *hueyi* are terrestrial, although *elegans* is partly aquatic in parts of its range, and that *vagrans* feeds on both aquatic and terrestrial animals. Because of its generalized morphology and ecology Fitch regarded *vagrans* as primitive and the probable ancestor of the artenkreis.

The Hydrophila group included the intergrading forms *T. o. hydrophila*, *T. o. couchii*, *T. o. gigas*, and the isolated *T. hammondi* and *T. digueti*. The members of the group are primarily aquatic, in that they go into the water to seek their food and to escape from their enemies. "All are characterized by medium to very large size, narrow, pointed head, with posterior supralabials and salivary glands reduced in size, dull colors with checkered or monotone patterns..." (Fitch, 1940:128).

The Ordinoïdes group included two intergrading forms, *T. o. ordinoides* and *T. o. atratus*. The group "is characterized by medium or small size, reduced scutellation, bright colors, terrestrial tendencies, and restriction to humid habitats" (Fitch, 1940:129).

Fitch demonstrated that these three groups are joined to one another by intergrading populations. The *Ordinoides* group is connected to the *Elegans* group by intergradation of *atratus* and *elegans*. The *Hydrophila* group is united to the *Elegans* group by intergradation of *hydrophila* and *biscutatus*.

Since the publication of the 1940 revision by Fitch, however, certain changes in taxonomy have been suggested. Mayr (1942) was the first to criticize Fitch's interpretation of the "*ordinoides* artenkreis." He regarded its three subgroups as morphological and biological units connected only by weakly hybridizing populations and suggested that they be recognized as three distinct species. Johnson (1947) described a population of garter snakes from western Washington and British Columbia which he named *Thamnophis elegans nigrescens*. In the same paper he designated the *Ordinoides* group as a distinct species and applied the name *elegans* as the specific name of the *Elegans* group. He suggested, as had Mayr, that the *Hydrophila* group was probably also a distinct species. But he presented no new data in support of this change in taxonomy.

Both Mayr and Johnson evidently suggested these changes because they were disturbed by the frequent occurrence of two or three subspecies of the same species in the same area. Fitch (1948), supported by Fox (1948), criticized their interpretation of this problem. Fitch emphasized that the three subgroups of the artenkreis are connected by smoothly intergrading populations and there is no justification for separating them. Fox (1948) eliminated part of the complication of overlapping ranges of subspecies by showing that *Thamnophis ordinoides ordinoides* is a distinct species. Fitch (1940) and Van Denburgh and Slevin (1918) had described intergradation between the races *ordinoides* and *atratus*, although Fitch recognized that the "intergradation" was sharp and needed further checking. On the basis of range overlap and distinct morphological differentiation which was substantiated by the examination of many broods of both forms, Fox (1948) suggested that *ordinoides* did not interbreed with *atratus*. He applied the name *Thamnophis elegans*, which Johnson (1947) had revived, to the remaining forms of the rassenkreis. But Fox retained *atratus* in subspecific relationship with the race *elegans* with which it intergrades.

Fitch (1948), in discussing the race *T. e. nigrescens* described by Johnson (1947), pointed out that this population had already been analyzed in his monograph. He reiterated that it was only weakly differentiated from the parent population of *vagrans* and did not merit subspecific distinction.

Smith (1942) described a form of garter snake from Chihuahua and Durango, Mexico, which he named *Thamnophis ordinoides errans*. Fitch (1948), in reviewing the relationship of this form to the *ordinoides* complex, recognized a possible affinity to *vagrans*; but because of certain morphological differences and the great geographic isolation of the Mexican snake, he felt that it might best be designated as a distinct species, *Thamnophis errans*.

In the same paper, Fitch (1948) presented new data which suggested intergradation between two forms originally considered to be geographically isolated, *T. o. couchii* and *T. hammondi*. On the basis of this new evidence he reduced *hammondi* to the rank of subspecies. Although he regarded *T. digueti* as being clearly a member of the *Hydrophila* group, he classified it as a distinct species because of its geographic isolation and morphological differentiation.

The forms of *ordinoides-elegans* garter snakes recognized in the last published systematic review of this subject (Fitch, 1948) are:

Thamnophis ordinoides (Baird and Girard)
Thamnophis elegans elegans (Baird and Girard)
Thamnophis elegans atratus (Kennicott)
Thamnophis elegans hueyi Van Denburgh and Slevin
Thamnophis elegans vagrans (Baird and Girard)
Thamnophis elegans biscutatus (Cope)
Thamnophis elegans hydrophila Fitch
Thamnophis elegans couchii (Kennicott)
Thamnophis elegans gigas Fitch
Thamnophis elegans hammondi (Kennicott)
Thamnophis diegueti (Mocquard)
Thamnophis errans Smith

PROPOSED CHANGES IN TAXONOMY

In the vicinity of San Francisco Bay there are three major types of garter snakes which superficially appear to be separate species since they do not interbreed. One of these is the clearly distinct species *Thamnophis sirtalis*. The two other major forms in the region have until recently been regarded as color phases of the same subspecies, *T. elegans atratus*. Recent intensive collecting and field study have revealed many additional differences and have afforded evidence that these forms do not interbreed. They are morphologically and ecologically distinguishable, one being terrestrial and the other aquatic. Although they do not interbreed, they are linked by a chain of interbreeding races and apparently represent divergent subspecies of the *Thamnophis elegans* rassenkreis. Fitch (1940) based his description of the relationships of *atratus* to *elegans* and to *ordinoides* on specimens with terrestrial habits. However, the type specimen of *atratus* is of the aquatic form. I therefore retain the name *atratus* for the aquatic form and apply a new subspecific name, *terrestris*, to the terrestrial form. Another new subspecies, *T. e. aquaticus*, is morphologically and geographically intermediate between *atratus* and *hydrophila*.

I further suggest that the species *Thamnophis elegans* be divided into two morphologically and ecologically recognizable groups instead of into the three proposed by Fitch. This new scheme would retain the terrestrial and the aquatic groups essentially as described by Fitch but would allocate the races of his unspecialized *Elegans* group to one of these major subdivisions. Although these two groups appear to be sympatric, polytypic species, they should be regarded as a single species since they are connected by smoothly intergrading populations.

The group designated as aquatic in this study contains the forms *atratus*, *aquaticus*, *gigas*, *hydrophila*, *biscutatus*, *couchii*, *hammondi*, and *diegueti*. The group designated as terrestrial contains the forms *terrestris*, *elegans*, *hueyi*, *vagrans*, and *nigrescens*.

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Professor R. C. Stebbins kindly contributed the drawings in figure 10.

MATERIALS AND METHODS

Large series of specimens were collected from various localities around San Francisco Bay and adjacent regions. Notes on habits and behavior were recorded at the time of collection. For most specimens, notes on general color and pattern were recorded from the living animal. In this paper the color nomenclature of Ridgway (1912) is used for more exact descriptions, and his color names are capitalized.

Most of the specimens have been added to the collection of the Museum of Vertebrate Zoology, University of California, which supplied much of the material analyzed in this paper. Specimens in the collections of the California Academy of Sciences and the Stanford Natural History Museum were also examined.

Morphological characters upon which descriptions are based are color, pattern, scutellation, and proportions. The characters of scutellation used are those routinely employed in studies of geographic variation in snakes: number of gastrosteges or ventrals; number of urosteges or subcaudals; number of rows around the body at the neck, thoracic, and posterior body regions; and number of supralabials, infralabials, preoculars, and postoculars. In many instances the body and tail of freshly killed specimens were measured. These measurements were recorded in millimeters.

Certain samples were also analyzed to determine the proportions of the parts of the head. The small size of the areas involved required the use of dial calipers. Measurements were taken from preserved specimens as follows: head length, taken from behind the angle of the jaw to the tip of the rostral; gape, from the posterior end of the labials to the tip of the rostral; width of head, taken at three points: (1) greatest width, which occurs in the posterior region of the jaws, (2) interorbital width, measured from the external margins of the supraoculars, (3) width of the rostral; relative length of internasals, determined by the ratio of the length to the width at the posterior margins; relative height of sixth and seventh supralabials, determined by ratio of greatest height to greatest length. The following ratio proposed by Fitch (1940:15) was also used for certain comparisons:

$$\frac{\text{Width of combined contact of both internasals with rostral}}{\text{Width of contact of left (or right) nasal with rostral}}$$

All statistical data were graphed for the purpose of easy comparison of samples. Mean, standard deviation, standard error, and coefficient of variation were calcu-

lated for each sample. Tests of significance used were those of Dice and Leraas (1936) and the t test (see Snedecor, 1940). A probability of less than 1 per cent is regarded as highly significant in the latter test.

Abbreviations used in subspecies accounts: CAS, California Academy of Sciences; MVZ, Museum of Vertebrate Zoology; SBNHM, Santa Barbara Natural History Museum; SNHM, Stanford University Natural History Museum; WF, Wade Fox.

ACCOUNTS OF SUBSPECIES

THE AQUATIC GROUP

Thamnophis elegans atratus (Kennicott)

Eutainna atrata Kennicott, 1860: 296, original description.

Eutaenia infernalis vidua Cope, 1892: 658.

Tropidonotus ordinatus var. *infernalis*, Boulenger, 1893: 207, part.

Thamnophis elegans, Van Denburgh, 1897: 207, part.

Eutaenia elegans elegans, Brown, 1903: 288, part.

Eutaenia elegans infernalis, Ditmars, 1907: 226, pl. 69, fig. 2.

Thamnophis ordinoides ordinoides, Ruthven, 1908: 147, part.

Thamnophis ordinoides, Thompson, 1915: 351.

Thamnophis ordinoides atratus, Van Denburgh and Slevin, 1918: 224, part.

Thamnophis elegans atratus, Fox, 1948: 120, part.

Type.—Designated by Fitch (1940:89) as one of two cotypes on which the original description was based. Adult male, United States National Museum no. 970-A, collected at San Francisco, California, by R. D. Cutts.

Original description.—(From Kennicott, 1860: 296) :

EUTAINIA ATRATA, Kennicott.

SP. CH.—Body compact, cylindrical, moderately stout. Head small and narrow, eye very small; eight upper labials sixth largest. Dorsal rows of scales seventeen, exterior row largest, higher than long, and very slightly carinated; the next row smaller, but considerably larger than the third, distinctly carinated. Scales of the central dorsal rows proportionately shorter than in *E. concinna* and *E. prokeringi*. A very broad, deep lemon yellow dorsal stripe, covering nearly three rows, and distinct from head to tip of tail. The rest of the upper parts entirely deep blue black, without a trace of the lateral stripe or of light spots. Abdomen entirely uniform greenish slate, yellowish green under the head.—Kennicott.

California.—C.

Range.—Common in coastal mountains from San Luis Obispo County, California, north to San Francisco peninsula; less common east of San Francisco Bay to Carquinez Strait and Sacramento River. Found eastward as far as Pinnacles National Monument in San Benito County, Hospital Canyon of western San Joaquin County, Romero Creek of western Merced County, Mount Hamilton in Santa Clara County, Arroyo Mocho in eastern Alameda County, and Mount Diablo in Contra Costa County (fig. 1).

Diagnosis.—A short, somewhat stout garter snake with pointed snout and remarkably uniform head scales: almost always 8 upper labials, 10 lower labials, 1 preocular, and 3 postoculars on each side (table 2). Internasals usually longer than broad, pointed anteriorly, and in narrow contact with rostral; sixth and seventh upper labials relatively large and taller than long, resembling those of terrestrial

rates rather than those of other aquatic rates, in which rows of upper labials are practically straight.

Broad orange or orange-yellow dorsal stripe usually covers at least $\frac{2}{3}$ -1- $\frac{2}{3}$ rows of scales, frequently 3 full scale rows, and occasionally only central row involved. Lateral stripes absent in blue-black individuals from San Francisco peninsula, but elsewhere usually present and conspicuous pale yellow.



Fig. 1. Map of California coast from San Francisco Bay to Santa Barbara showing locality records of *T. e. atratus*.

Top of head usually olive, dark olive, or blue black; chin and throat bright lemon yellow, this color usually extending to or over lower labials; upper labials generally pale yellow. Iris very dark, almost black except for loose silvery network in most specimens. Dorsal ground color blue black, black, or dark olive with distinct or indistinct black spots; no red spotting. Ventral surface varies from deep blue to pale blue or green; in most specimens central part of each ventral scute irregularly blotched with Salmon-Orange or Capucine Orange. Blotching begins in anterior third of body and increases posteriorly.

Maximum number of body scale rows, 19; always 19 at neck and thoracic regions; almost always 15 at posterior end of body, rarely 17. Ventral scutes range from 145 to 169 in males and from 138 to 167 in females; caudal scutes range from 70 to 89 in males and 64 to 82 in females.

Comparison with other forms.—*T. e. atratus* intergrades with *T. e. aquaticus* and occupies parts of the ranges of *T. e. terrestris* and *T. e. hammondi*. For comparisons with *aquaticus* and *terrestris*, see sections dealing with these forms.

In geographically overlapping *atratus* and *hammondi* color differences very distinct: dorsal stripe in *atratus* broad and brightly colored, in *hammondi* absent or confined to neck region; dorsal ground color black or olive drab in *atratus*, brown or olive gray in *hammondi*; dorsolateral blotches distinct and well represented in *hammondi*, obscure in *atratus*. *Hammondi* lacks lemon-yellow throat characteristic of *atratus*.

Both races have pointed internasals longer than wide, a character common throughout the aquatic group. Sixth and seventh supralabials relatively large and taller than long in *atratus*, longer than tall in *hammondi*. Nineteen and 15 scale rows at thoracic region and posterior end of body, respectively, characteristic of *atratus*; 21 and 17 characteristic of *hammondi*. In *hammondi*, average numbers of gastrosteges and urosteges higher than in *atratus*. In *hammondi*, preoculars frequently divided and eyes large; in *atratus*, preoculars rarely divided, diameter of eye small.

Geographic variation and relationships.—It is difficult to explain the color variation within this subspecies. Perhaps the following correlations are significant. Specimens from the more arid parts of the range, that is, the East Bay region, Mount Diablo, Arroyo Mocho in Alameda County, Mount Hamilton, the Pinnacles National Monument, western San Joaquin County, and Merced County, show marked similarity. They have distinct lateral stripes and a dorsal stripe of moderate width. Most of them are larger and have a paler ventral color and higher scale counts than the coastal populations. Although from a coastal location, specimens from Monterey County are similar in color to those from the inland localities mentioned above. A sizable population with a characteristic color pattern is represented by specimens from the northern Santa Cruz Mountains and the San Francisco peninsula. These animals are blue black above and only slightly paler below. Their dorsal stripe is broad and orange, and they usually have no lateral stripe. They are most frequently found around the ponds, lakes, and small streams which characterize this area. It is worthy of note that specimens of the race *T. e. aquaticus* in the coastal parts of Marin and Sonoma counties are markedly similar to them in coloration. Since the two groups are somewhat removed geographically, this appears to be the result of convergence.

There can be no reasonable doubt that *T. e. atratus*, as now defined, is related to the aquatic group (*Hydrophila* group of Fitch) of garter snakes which includes the subspecies *hydrophila*, *couchii*, *gigas*, and *hammondi*. It is related to this group through intergradation with *T. e. aquaticus*. The area of intergradation of these two races occurs in the vicinity of Carquinez Strait and the Sacramento River. Specimens from near Vallejo and Vacaville, Solano County, are intermediate in color and show some enlargement of the posterior labials; this suggests an affinity

to *atratus*. The natural division created by the Sacramento River and Carquinez Strait seems to be the most suitable place for dividing the two races. Specimens from the area of intergradation are not numerous.

Although the range of *T. e. gigas* lies to the east of that of *T. e. atratus*, and the forms are ecological counterparts as well as allopatric subspecies, I have no evidence that their ranges come together or that there is any intergradation. They are extremely distinct morphologically. In the southern part of its range, *atratus* apparently occupies the same area as another aquatic garter snake, *T. e. hammondi* (fig. 6). I have no detailed field data on the ecological relationships of the two, but it seems likely that they offer competition to each other since they are both aquatic in their habits. It is probable that *hammondi* prefers large, open streams and rivers, whereas *atratus* prefers small streams and ponds. Because of this overlap in ranges, Monterey and San Luis Obispo counties have three races of garter snakes of the species *T. elegans* as well as one of *T. sirtalis*.

Ecology.—*T. e. atratus* is basically an aquatic garter snake. Throughout its range there are not as many large rivers and swift streams as there are in the ranges of *hydrophila* and *couchii*. Most of the *atratus* specimens which I collected were taken in the vicinity of ponds, lakes, or small streams. This limited, sluggish-water habitat may account for the fact that the body is shorter and stouter than it is in races like *hydrophila* which inhabit larger, swifter streams. The different head shape of these two races may also be correlated with this difference in habitat, or possibly with the difference in feeding habits. *Hydrophila*, with a longer snout and jaw, feeds mostly on fish, whereas *atratus* feeds chiefly on tadpoles and frogs.

The diet of *T. e. atratus* consists entirely of aquatic or amphibious animals. Small frogs (*Rana aurora*), tadpoles, *Triturus torosus*, and one small mass of fish eggs were found in the stomachs of captured specimens. Undoubtedly, this race also eats fish when that food is available. To my knowledge, this is the only form of garter snake that feeds on the adult, west coast *Triturus*. In the laboratory this race fed on all the local species of frogs and salamanders as well as on various commercial fish. It would not eat small rodents and slugs.

I found no indication that the character of the vegetation is of any vital significance to these snakes. They occur in areas of dense vegetation and in areas of sparse vegetation such as Pinnacles National Monument. In areas where vegetation is sparse their major problem is how to escape from the heat; where it is dense they require breaks in the vegetation which allow penetration of sunlight. I found them most abundant on grassy slopes near small ponds. Their chief ecological requirement appears to be the presence of suitable food. However, small populations of this race are present in areas where the streams are small and intermittent and the food supply is low, for example on the upper oak- and chaparral-covered slopes of Strawberry Canyon east of Berkeley. No recognizable food items could be recovered from specimens collected in this area, and it is difficult to see how the snakes find sufficient food. The only known acceptable food items in this vicinity are plethodontid salamanders, and a few *Triturus* and *Hyla*. Since *T. e. terrestris* is much more abundant than *atratus*, and competition between them for the terrestrial and amphibious food species must be severe, the relative scarcity of *atratus* in the Berkeley hills is not surprising.

Records of occurrence.—CALIFORNIA: *Contra Costa Co.*—2 mi. SW Walnut Creek (MVZ 1); Moraga Valley (MVZ 1); Mount Diablo (MVZ 1); Rock City Camp, near summit Mount Diablo (MVZ 1); Las Trampas Creek, St. Mary's College (MVZ 1); Wildcat Canyon (MVZ 7). *Alameda Co.*—Vicinity of Berkeley (MVZ 12); Old Redwood Canyon (MVZ 1); Arroyo Mocho (MVZ 9). *San Joaquin Co.*—Hospital Canyon, 500 ft. (MVZ 2). *Stanislaus Co.*—Orestimba Creek (MVZ 1). *Merced Co.*—Romero Creek, 4 mi. W Hill Ranch (MVZ 2). *San Francisco Co.*—(MVZ 13). *San Mateo Co.*—Skyline Blvd., 3–6 mi. S San Francisco Co. line (MVZ 38); San Andreas Lake (SNHM 6, MVZ 1); junction Tanforan Rd. and Skyline Blvd. (SNHM 1); Skylonda (SNHM 5); Eisenberg Ranch, Skyline Blvd., S La Honda Rd. (SNHM 6); summit, near Searsville (SNHM 3); Pilarcitos Lake (SNHM 2); Crockers Lake (SNHM 1); La Honda (SNHM 2); Corte Madera Creek (SNHM 1); Alpine Creek Ranch (MVZ 1); Menlo Park (MVZ 1); Mills Lake (SNHM 1); Butano basin (SNHM 1); Sharp Park (MVZ 3); Rockaway Beach (MVZ 1); Moss Beach (MVZ 1); 2 mi. S (MVZ 1), 3.1 mi. S (MVZ 3), and 5.8 mi. S (MVZ 2) Half Moon Bay; mouth San Gregorio Creek (WF 1); Pescadero Creek basin (SNHM 1); Pescadero (SNHM 2); 2½ mi. N Pigeon Point (MVZ 1); 2 mi. N Point Año Nuevo (MVZ 3). *Santa Clara Co.*—Stanford University (SNHM 8); Palo Alto (CAS 1); Gilroy Hot Springs (CAS 2); San Jose (CAS 2); Smith Creek, Mount Hamilton (SNHM 1); Uvas Creek (SNHM 1); Coyote Creek, near head canyon (SNHM 1); 12 mi. from summit Mount Hamilton toward Livermore (SNHM 1). *Santa Cruz Co.*—Little Creek, 1 mi. NNE Swanton (MVZ 1); Big Creek, 2½ mi. ENE Swanton (MVZ 5); Santa Cruz (MVZ 1); Soquel (SNHM 3); mouth Scott Creek (MVZ 1); Waddell Creek (MVZ 12, SNHM 4); Boulder Creek (SNHM 1, MVZ 2); near Zayante (SNHM 2). *San Benito Co.*—Pinnacles National Monument (CAS 1). *Monterey Co.*—Pine Creek, head Little Sur River (MVZ 2); Turner Creek, 1 mi. W Devils Peak (MVZ 1); Malpaso Creek, 5 mi. S Carmel (MVZ 1); Carmel (CAS 6); Seaside (CAS 4); Carmel River (SNHM 2); Pacific Grove (SNHM 4, MVZ 3). *San Luis Obispo Co.*—Morro (CAS 1); Oceano (CAS 1); 3.5 mi. NW San Luis Obispo (MVZ 1).

***Thamnophis elegans aquaticus* subsp. nov.**

Thamnophis elegans, Van Denburgh, 1897: 207, part.

Thamnophis ordinoides ordinoides, Ruthven, 1908: 147, part.

Thamnophis ordinoides atratus, Van Denburgh and Slevin, 1918: 224, part.

Thamnophis ordinoides hydrophila, Fitch, 1936: 648, part.

Thamnophis elegans hydrophila, Fox, 1948: 120, part.

Type.—Adult male, Museum of Vertebrate Zoology no. 48196, collected at Dillon Beach, Marin County, California, by Wade Fox, July 18, 1949.

Description of type.—(Colors from freshly killed specimen.) Top of head Brownish Olive, somewhat more Olive on snout; iris grayish yellow with pale-yellow rim round pupil; supralabials Light Yellowish Olive above and Olive-Yellow below; central lower labials Colonial Buff; chin shield Marguerite Yellow; cheeks Light Yellowish Olive in region of posterior labials, yellow deepening posteriorly over cheeks to Apricot Yellow, which in turn continues into lateral stripes. Lateral stripes darken gradually behind neck, each occupying approximately complete second and third scale rows. Greater part of each scale in lateral stripe Sulphin Yellow, but anterior edges, particularly where second and third rows come together, Straw Yellow. Dorsal stripe occupies nearly 5 full rows at nape and 3 full rows over most of body; Deep Chrome in color. Dorsolateral region black with faint traces of Brownish Olive and very indistinct dorsolateral blotches. Interscale light spots Pale Olivine and present only between scales of more ventral rows; elsewhere, interscale skin black. First scale row and edges of gastrosteges Deep Olive; ventral scutes Tea Green anteriorly and Andover Green posteriorly with central Ochraceous-Salmon suffusions.

Internasals pointed and longer than wide; sixth and seventh supralabials only slightly enlarged and about as long as tall; preoculars number 1-1, postoculars 3-3, temporals 1-2-2 on each side. Nineteen scale rows at neck, 19 at thoracic region, and 15 at posterior end of body. Gastrosteges, 157; undivided anal plate; urosteges, 77. Terminal scale of tail apparently missing. Total length, 585 mm.; tail length, 145 mm.

Range.—California coast from Golden Gate to Gualala River at Mendocino Co. line; Coast Ranges in this area as far north as South Fork of Eel River; southern

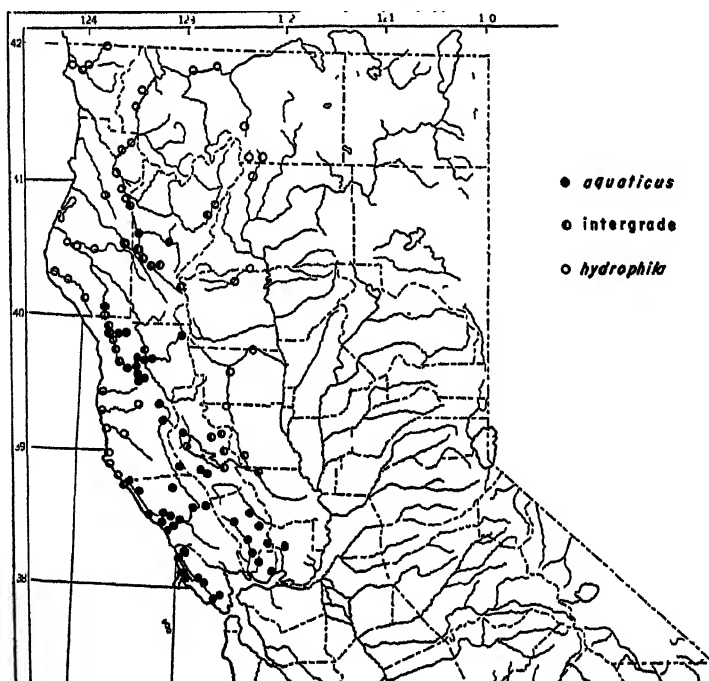


Fig. 2. Map of northern California showing locality records of *T. e. aquaticus*, *T. e. hydrophila*, and their intergrades within California.

and southeastern tributaries of Eel River, and narrow area extending northward into southwestern Trinity County to southern tributaries of Trinity River; along north shore of San Francisco Bay eastward to Sacramento Valley and northward into Lake and Colusa counties (fig. 2).

Diagnosis.—Aquatic garter snake with relatively long, slender body, long head and gape, pointed internasals, and narrow rostral. Relatively straight upper labials, neither strikingly elevated nor enlarged in region of sixth or seventh.

Yellow, orange, or orange-yellow dorsal stripe ranges from at least $1\frac{1}{2}$ -1- $\frac{1}{2}$ scale rows to 3 full scale rows. Lateral stripe always present and distinct (except in certain intergrades with *hydrophila*), light olive buff frequently with olive-yellow or apricot-orange spots.

Head mostly dark olive, with or without black pigment in parietal region; upper labials usually olive, fading ventrally to pale buff or cream of lower labials;

usually an apricot-orange area covering cheek behind jaw. Chin usually pale cream or pale yellow, although many specimens have lemon-yellow throat. Iris gray or drab, except near range of *hydrophila*, where it may be brown. Dorsolateral ground color drab, dark olive, or nearly black; darker pigment extensive, giving general impression of extremely dark back, although some specimens have faint patches of lighter olive. Ventral surface usually of various shades of light blue or green, becoming darker posteriorly; varying amounts of pale salmon in central portions of ventral scutes, the color tending to increase in amount posteriorly.

Dorsal scale rows 19-19-15 or 19-19-17, rarely 19-21-17. Ventral scutes range from 142 to 167 in females, 147 to 167 in males; caudal scutes from 63 to 82 in females, 74 to 93 in males.

Comparison with other forms.—*Thamnophis elegans aquaticus* distinguishable from *T. e. atratus*, with which it intergrades, by shape of sixth and seventh supralabials. In *aquaticus* these scutes longer than tall; in *atratus* more strikingly enlarged, usually taller than long (fig. 8), and extend dorsally behind lower postocular. Lipochrome suffusions on ventral surface salmon (Ochraceous-Salmon) in *aquaticus*, nearly orange (Salmon-Orange or Capucine Orange) in *atratus*; cheeks generally orange tinted (Ochraceous-Orange) in *aquaticus*, pale orange yellow or lacking lipochrome pigmentation in *atratus*. Iris gray, or brown in northern parts of range of *aquaticus*, dusky in *atratus*. One-third to one-half the *aquaticus* population have more than 15 scale rows at posterior end of body, *atratus* as a rule has only 15. Numbers of gastrosteges and urosteges significantly greater in *aquaticus*, except that average in *atratus* from interior parts of range is as high as in any population of *aquaticus* (fig. 10). Both races characterized by relatively small types along coast and large types in interior.

T. e. aquaticus resembles *T. e. hydrophila* in body proportions, shape of head, and shape of posterior labials and internasals (figs. 8 and 9). But ground color nearly black instead of olive gray or olive brown, and dorsal surface has not checker-board appearance of typical *hydrophila*. Dorsal stripe of *aquaticus* always present, of various shades of orange or yellow, covers at least $1\frac{1}{2}$ -1- $1\frac{1}{2}$ scale rows; dorsal stripe of *hydrophila* almost completely absent or very indistinct, always dull in color, occupies at most only middorsal scale row and edges of some adjacent scutes. Lateral stripes always present and pronounced in *aquaticus*, frequently absent or poorly defined in *hydrophila*. Both races have Ochraceous-Salmon belly. *Hydrophila* tends to have greater numbers of scale rows around the body (table 1), and more gastrosteges and urosteges. Considerable range overlap exists between the two races (figs. 11 and 12).

Many specimens of *T. e. aquaticus* closely resemble *T. e. biscutatus* in color and shape. Both races have broad dorsal stripes, black ground color, distinct lateral stripes, and relatively long pointed heads. In *aquaticus* head more pointed and internasals longer and more pointed. Sixth and seventh supralabials enlarged in *biscutatus*, not in *aquaticus*. Former lacks Ochraceous-Salmon belly and pale-yellow or lemon-yellow throat frequently present in *aquaticus*. *Biscutatus* has maximum of 21 or 23 scale rows around body, *aquaticus* rarely varies from 19. Counts of urosteges and gastrosteges higher in *biscutatus*. *Biscutatus* usually has divided preoculars, a condition rare in *aquaticus*.

T. e. aquaticus overlaps part of the ranges of *T. e. terrestris* and *T. e. elegans* but does not interbreed with either. Although *aquaticus* is basically distinct from these races both morphologically and ecologically, it is easily confused with them because of superficial similarities. Comparison with *terrestris* will be deferred until *terrestris* has been described, but similarities and differences of *aquaticus* and *elegans* should be pointed out at this time.

T. e. aquaticus and *T. e. elegans* occur together in interior Coast Ranges of Mendocino and southwestern Trinity counties. Both have a broad, yellow dorsal stripe, that of *elegans* being far brighter; lateral stripes of *elegans* are also more pronounced. *Elegans* has blunt internasals usually wider than long, contrasting with long, pointed internasals of *aquaticus*. Sixth and seventh supralabials enlarged and usually taller than long in *elegans*, smaller and longer than tall in *aquaticus*. *Elegans* lacks Ochraceous-Salmon suffusion present on belly of *aquaticus*; throat of latter usually pale or lemon yellow, that of former whitish. In *elegans* almost always a maximum of 21 scale rows, in *aquaticus* only 19.

Geographic variation and relationships.—*T. e. aquaticus* is most closely related to the races *hydrophila* and *atratus* with which it intergrades. In physical characteristics and geographic position it is intermediate between *hydrophila* to the north and *atratus* to the south. Although it resembles *atratus* in many color characteristics, in morphology it resembles *hydrophila*. It intergrades with the latter in northern Sonoma County and southern Mendocino County at the coast. Inland, along the Gualala River, *hydrophila* occurs up the north branch and *aquaticus* up the south branch. The intergradation is abrupt at the mouth of the Gualala River. All streams south of the Gualala River are inhabited by rather typical *aquaticus*, all north of it have typical *hydrophila*. Just east of the first Coast Ranges, the zone of intergradation shifts to the north. Intergrades are present at the southern end of the South Fork of the Eel River near Branscomb, at the mouth of Rattlesnake Creek near Cummings, and along the South Fork of the Eel River at least twelve miles northwest of Cummings. And specimens with a broad dorsal stripe occur sporadically as far north as Stephens Grove State Park in Humboldt County, though typical examples of *hydrophila* have been found at several points along the river south of this area. *Aquaticus* is present in the small streams leading into the South Fork of the Eel River from the east and south, but only typical *hydrophila* or intergrades are found in the main stream. *Hydrophila* approaches the river from the west and north, and apparently selection favors the *hydrophila* characters in the larger stream. The peculiar spotty distribution of the intergrades is probably due to the fact that snakes with *aquaticus* characteristics enter the main stream only from the small southern and eastern tributaries. The change from *aquaticus* to *hydrophila* in this region is not gradual. The principal characters in which they differ appear to be of a discontinuous nature. Several specimens from this area of intergradation have considerable red spotting along the sides of the body, a feature that is extremely rare among the aquatic races. It is highly unlikely that this spotting indicates interbreeding of these aquatic forms with the normally red-spotted *terrestris*, for the latter race is morphologically very different. Rather, this and the irregularities in the pattern of intergradation suggest that the South Fork of the Eel River represents an area of secondary intergradation between *aquaticus* and *hydrophila*.

Intergradation occurs farther east in Mendocino County, near Dos Rios, where the Middle Fork and South Eel River join to form the main Eel River. Intergrades were found both near this junction and a few miles downstream. Specimens from Outlet Creek and the South Eel River are typical *aquaticus*, as are those from the Middle Fork of the Eel River. Only a few specimens are available from this area at present. The eastern and northern tributaries of the Middle Fork of the Eel River afford *aquaticus* access to southwestern Trinity County. It apparently crosses the low hills between these tributaries and the southern tributaries of the Trinity River. Specimens with a broad dorsal stripe are found in this part of the Trinity drainage as far north as Hyampom. Actually, it seems best to regard these specimens as *hydrophila-aquaticus* intergrades, at least those from the more northern localities.

Lake County offers a special problem in the unraveling of the relationship of *aquaticus* to *hydrophila*. Three specimens which are clearly *aquaticus* were collected on the south side of Clear Lake; another similar specimen was collected near Upper Lake. All four show only the slightest tendency toward *hydrophila* and scarcely deserve the designation of intergrades. However, Museum of Vertebrate Zoölogy no. 36268, taken at Lakeport by John Davis, is characteristic of *hydrophila* in every respect. The accuracy of the collecting data is unquestionable. Although it is possible that the Lakeport specimen was introduced, I feel that until the introduction is proved, this record of occurrence should be considered valid and that an attempt should be made to account for its presence. Perhaps the single specimen from Upper Lake is misleading in its similarity to *aquaticus* and this population is actually an intergrading population. Specimens from Bartlett Springs, just north of the eastern end of Clear Lake, are suggestive of *aquaticus* in many ways yet show definite affinities to *hydrophila*. *Hydrophila* influences conceivably could reach the west end of the lake from the northeast between Bartlett Springs and Upper Lake; this might account for the Lakeport specimen. Aquatic garter snakes appear to be rare around the lake itself, and most specimens have been collected from small streams and creeks in the vicinity.

North of Bartlett Springs there is a further transition toward *hydrophila*. Specimens from southwestern Colusa County are suggestive of *aquaticus*, those from Stonyford tend strongly toward *hydrophila*, and typical *hydrophila* are present in Glenn County along Stony Creek. Specimens in the northern Sacramento Valley appear to be *hydrophila-couchii* intergrades. Farther south in the Sacramento Valley near Gridley, Butte County, there is indication of an intergradation between *aquaticus* and *gigas*. This relationship is suggested by specimens which have the broad dorsal stripe characteristic of *aquaticus* but have the 23 scale rows characteristic of *gigas*. Specimens from the region of Vacaville, Solano County, show no indication of intergradation with either *hydrophila* or *gigas*, but there may be a slight tendency toward *atratus*. These forms are probably best characterized as typical *aquaticus*. Because the transition from *aquaticus* to *atratus* is gradual, I have not designated intergrading specimens; rather, I have arbitrarily divided the two races at San Francisco Bay and the Sacramento River, since these form a natural geographic break.

Within the race *aquaticus*, the geographic variation of the dorsal stripe is very marked. A relatively broad, orange dorsal stripe is found in *aquaticus* in Sonoma,

Marin, and Napa counties and in part at least of Solano County. Specimens near the area of intergradation with *hydrophila* have a yellow dorsal stripe of minimum width; those toward the Sacramento Valley, in northeastern Napa, Yolo, and Colusa counties, have a narrow stripe of dusky yellow.

Throughout the upper drainage of Rattlesnake Creek, a tributary of the South Fork of the Eel River, there is a restricted population of *aquaticus* the members of which have a lemon-yellow throat and chin like those of *atratus*.

Two interesting specimens from the coastal part of Sonoma County completely lack lateral stripes, but have an orange dorsal stripe on a black background as do typical *aquaticus*. In color pattern these specimens are amazingly similar to the *atratus* found in San Mateo County. I do not think that the similarity is due to intergradation of these two races, nor that it is a mere case of convergence. Rather, I feel that the pattern may be a result of intergradation with *hydrophila*, which frequently lacks lateral stripes, since specimens of typical *hydrophila* have been found only thirty miles north of where the two specimens were taken.

Ecology.—*T. e. aquaticus* appears to be similar to *hydrophila* (see Fitch, 1940: 57–58) in its habits. There is some indication that it will tolerate ponds and smaller and more sluggish streams more readily than typical *hydrophila* will, yet this may be a result of necessity rather than an expression of an actual preference. Examination of stomach contents reveals that *aquaticus* feeds primarily on fish, tadpoles, and frogs.

Records of occurrence.—CALIFORNIA: *Humboldt Co.*—South Fork Eel River, Stephens Grove State Park (MVZ 2); * East Fork Campground, Willow Creek (MVZ 7); * Cobbs (MVZ 12). * *Trinity Co.*—White Rock Ranger Station (MVZ 1); * 2 mi. W Iiyampom (MVZ 2); * 12 mi. N North Yolla Bolly Mtn. (MVZ 1); * 3 mi. NNW Mad River Bridge, South Fork Mtn. (MVZ 2); * 2 mi. E Hayfork (MVZ 1); * Mad River Campground (MVZ 2); * Trinity River, 12 mi. S Trinity Center (MVZ 5); * mouth Granite Canyon, South Fork River (MVZ 3); * 2 mi. W Forest Glen (MVZ 1); * mouth North Rattlesnake Creek, 2.5 mi. E Forest Glen (MVZ 1); * Corn Creek, 5.5 mi. E Hayfork (MVZ 1). * *Mendocino Co.*—Rattlesnake Creek, 1 mi. S (MVZ 11) and 5 mi. SW (MVZ 7) Cummings; Outlet Creek, 8.7 mi. N Willets (MVZ 1); Outlet Creek, 1½ mi. S mouth, 2 mi. S Dos Rios (MVZ 1); Eel River, 1 mi. N Dos Rios (MVZ 2); * Middle Fork Eel River, 1½ mi. E Dos Rios (MVZ 4); Middle Fork Eel River at Jumpoff Creek (MVZ 6); 10 mi. S Willets (MVZ 1); 5 mi. N (MVZ 3), 6 mi. S (MVZ 2), 7 mi. S (CAS 1), and South Fork Eel River, 8–10 mi. W (MVZ 7) Laytonville; Robinson Creek, near Ukiah (MVZ 1); Sherwood (MVZ 4); Baldhill (MVZ 1); South Fork Eel River, 12 mi. N Cummings (MVZ 53); * 9 mi. W Cummings (MVZ 29); * at bridge on road to Rockport (MVZ 18); * mouth Big Dan Creek (MVZ 14); * mouth Cedar Creek (MVZ 15); * mouth Rattlesnake Creek (MVZ 2); * Branscomb (MVZ 3); * mouth North Fork Gualala River (MVZ 8); * mouth Gualala River (MVZ 4); * Pieta Creek (MVZ 1). *Lake Co.*—High Valley Creek, 1 mi. SW Glenbrook, 4 mi. WNW Cobb (MVZ 3); Glenbrook (MVZ 1); Scotts Valley, 6 mi. W Upper Lake (MVZ 1); 1 mi. S (MVZ 2)* and 3 mi. E (MVZ 1); * Bartlett Springs; Lower Lake (MVZ 1); * Cache Creek, 6.5 mi. E Stubbs (MVZ 1). * *Colusa Co.*—2½ mi. S Wilbur Springs (MVZ 1). * *Sonoma Co.*—Wheatfield Fork Gualala River (MVZ 4); Knights Valley Creek, near Kellog (MVZ 1); mouth Kolmer Gulch, 1 mi. NNW Fort Ross (MVZ 2); mouth Russian Gulch, 2¾ mi. NW Jenner (MVZ 2); mouth Russian River (SNHM 4); near Skaggs Springs (CAS 16); Healdsburg (SNHM 1); 4 mi. S Cazadero (MVZ 1); Austin Creek (MVZ 1); Duncans Mills (CAS 4); Guerneville (SNHM 1); 1 mi. W Guerneville (MVZ 2). *Marin Co.*—Dillon Beach (MVZ 37); 4 mi. NNE Dillon Beach (MVZ 1); Lake Ranch, N Bolinas (MVZ 6); 1 mi. S (MVZ 1) and 1 mi. W (MVZ 1) Inverness; Abbotts Lagoon (MVZ 1); Point Reyes Station (MVZ 1); near San Anselmo (MVZ 1); Tocaloma (MVZ 1). *Napa Co.*—1 mi. E Yountville (MVZ 1); Soda Creek, 6 mi. SSW (MVZ 2) and 7 mi. SSW

* Intergrades.

(MVZ 6) Monticello; Pope Creek, 5 mi. NNW Monticello (MVZ 1); Beagle's Ranch, 3 mi. N Napa (MVZ 1); Jameson Canyon (MVZ 1); Curry Lake (MVZ 1); Berryessa Creek (MVZ 1, SNHM 4). *Solano Co.*—Suisun Creek, 3.5 mi. WSW Suisun (MVZ 1); Vacaville (MVZ 3). *Yolo Co.*—Rumsey (MVZ 1).*

THE TERRESTRIAL GROUP

Thamnophis elegans terrestris subsp. nov.

Eutamia ordinoides, Baird and Girard, 1853: 33.

Eutaenia elegans ordinoides, Cope, 1892: 654.

Eutaenia infernalis infernalis, Cope, 1892: 657.

Tropidonotus ordinatus var. *infernalis*, Boulenger, 1893: 207, part.

Thamnophis elegans, Van Denburgh, 1897: 207, part.

Eutaenia elegans elegans, Brown, 1903: 288, part.

Thamnophis ordinoides ordinoides, Ruthven, 1908: 147, part.

Thamnophis ordinoides, Thompson, 1915: 351.

Thamnophis ordinoides atratus, Van Denburgh and Slevin, 1918: 224, part.

Thamnophis elegans atratus, Fox, 1948: 120, part.

Type.—Adult female, Museum of Vertebrate Zoölogy no. 48197, collected at Strawberry Canyon, Berkeley, Alameda County, California, by Wade Fox, June 23, 1949.

Description of type.—(Taken from freshly killed specimen.) Iris Raw Umber with light orange-yellow ring around pupil; top of head through temporals Brownish Olive; upper labials and rostral Buff-Yellow; cheeks Pyrite Yellow; lower labials Straw Yellow; chin shields Marguerite Yellow. Dorsal stripe occupies 3 full scale rows at nape, but posteriorly only $1\frac{1}{2}$ - $1\frac{1}{2}$ scale rows, although many scales of 2 lateral rows yellow over $\frac{2}{3}$ or more of surface. Central row Mustard Yellow and inner halves of 2 adjacent rows Straw Yellow. Chartreuse Yellow lateral stripes occupy upper halves of second, and all of third, scale rows. Two rows of dark blotches present dorsolaterally on body; well defined throughout most of body length but indistinct posteriorly and on tail. Within blotches some scales partly Sepia but mostly black. Skin between scales within blotches black, between blotches of upper row mostly white with small areas of Flame Scarlet, between blotches of lower row mainly Flame Scarlet with little white showing. Scales between blotches English Red. Flame Scarlet covers much of lateral stripes, also present in small, scattered spots in dorsal stripe. Numerous blotches of Flame Scarlet on ventral surface throughout body and tail; a few small Flame Scarlet spots on labials, rostral, and nasals. Difference in shades of red apparently due to color of underlying pigments. Throat cream color anteriorly, grading into Pale Dull Green-Yellow posteriorly, which grades into Glaucous-Green on ventral surface of body. Laterally, gastrosteges Deep Olive-Gray over $\frac{1}{4}$ of their width. First scale row Dark Olive-Gray; anterior margin of first and second scale rows and gastrosteges irregularly marked with black. Urosteges Glass Green centrally, mixing with Olive-Gray laterally.

Scale counts as follows: supralabials, 9-8; infralabials, 10-10, with fifth on both sides divided into 3 smaller pieces; preoculars, 1-1; postoculars, 3-3; temporals, 1-2-3 on both sides; scale rows, 21-21-17; ventral scutes, 158; caudal scutes, 80.

* Intergrades.

Internasals blunt anteriorly and wider than long; sixth and seventh supralabials enlarged and taller than long. Total length, 641 mm.; head and body length, 485 mm.

Range.—Narrow strip along California coast from Santa Barbara County northward around east side of San Francisco Bay, continuing along coast to Oregon

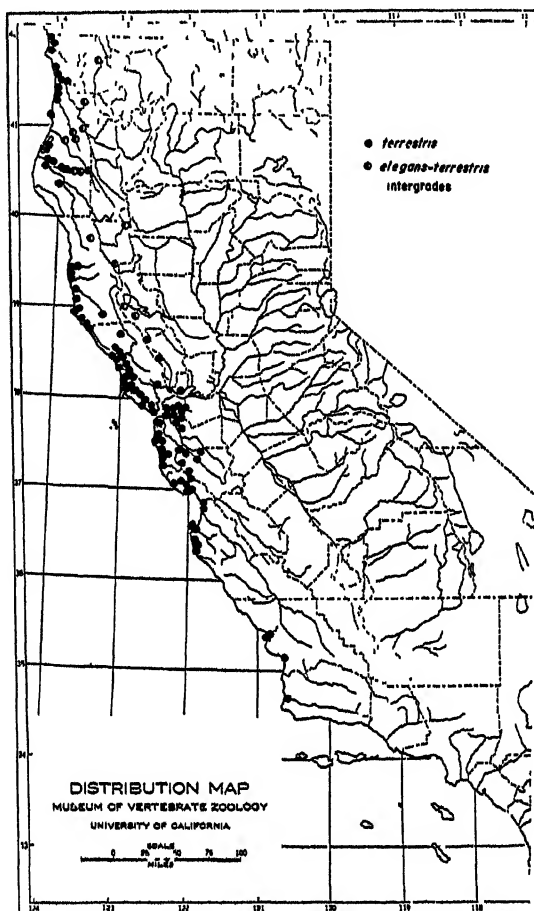


Fig. 3. Map of California showing locality records of *T. e. terrestris* and *T. e. elegans-terrestris* intergrades.

border (fig. 3). Range essentially that given by Fitch (1940) for *Thamnophis ordinoides atratus*.

Diagnosis.—Slightly stout garter snake with blunt, short snout; internasals shorter than wide, blunt anteriorly, and in broad contact with rostral; rostral broad; upper labials appreciably taller in region of sixth and seventh. Usually 8 upper labials and 10 lower labials, but not infrequently 7 and 9, respectively. Preoculars characteristically single but occasionally divided. Most frequently 3 postoculars, although 2 and 4 may occur.

Dorsal stripe yellow or yellow orange; appears to occupy exactly $\frac{1}{2}$ -1- $\frac{1}{2}$ scale rows, but appearance of regularity created by covering of outer half of two lateral rows by uppermost row of dorsolateral black blotches. Consequently, on many specimens, scales of lateral rows between consecutive blotches either yellow on both sides of keel, or red or olive on outer half. In specimens with essentially black dorsolateral region almost every scale of two lateral rows black on outer half. Lateral stripes conspicuous, dull olive yellow, but frequently varied amounts of red spotting superimposed on this.

Top of head usually olive brown or dark olive with small amount of black on parietals; upper labials pale yellow to olive buff; lower labials and chin approach cream buff. Iris brownish or sepia, sometimes appearing yellowish gray. Dorsolateral region either reddish brown with two distinct rows of regularly alternating black blotches and, at times, additional red spots; or black, dark olive, or olive brown with more or less indistinct black blotches. In reddish-brown individuals frequently interscale color outside of black blotches also reddish; otherwise these areas between blotches form characteristic interscale light spots. At Dillon Beach, Marin County, small numbers of individuals with blue-gray color phase occur; blue-gray ventral surface and dorsolateral regions apparently the only difference between these individuals and those with normal coloration. Ventral surface varies from pale shades of green to blue, with various amounts of red spotting. A few specimens lack red, but most have at least a few flecks somewhere on body.

Scale rows at neck almost always 19, rarely 21; maximum number in body region either 19 or 21; at posterior end of body characteristically 17, in rare instances 15. Ventral scutes range from 148 to 178 in males, 146 to 178 in females; caudal scutes from 71 to 90 in males, 61 to 88 in females. These numbers vary considerably in different parts of range (figs. 11 and 12).

Comparison with other forms.—*T. e. terrestris* occupies part of ranges of *T. e. atratus*, *T. e. aquaticus*, *T. e. hammondi*, and *T. ordinoides* without interbreeding. It intergrades with *T. e. elegans*.

T. e. terrestris distinguishable from *T. e. atratus* by shape of internasals. In former, internasals usually shorter than wide, and combined internasal contact with rostral usually greater than contact of either nasal with rostral; in *atratus*, length usually exceeds greatest width (fig. 8), and combined contact with rostral usually less than contact of either nasal. *Terrestris* usually has brown iris, cream-colored throat, and considerable red pigment scattered over sides and belly; *atratus* has dusky iris, almost invariably lemon-yellow throat, and lacks true red coloration although usually has areas of salmon orange in central parts of many ventral scutes. A few specimens from interior margin of range of *terrestris* lack red or brown pigment and resemble *atratus* in color. However, dorsolateral regions of former commonly reddish brown with conspicuous black blotches; in *atratus* these regions blue black, black, or dark olive, and lateral blotches usually not discernible. Dorsal stripe of *atratus* characteristically orange and frequently extends over 3 full scale rows, although it may be orange yellow and may vary in width. Dorsal stripe of *terrestris* usually yellow or, less frequently, orange yellow; fairly constantly occupies $\frac{1}{2}$ -1- $\frac{1}{2}$ scale rows. *Terrestris* most commonly has 21 and 17 scale rows at thoracic region and posterior end of body, respectively; *atratus* usually only 19

and 15 (table 1). Where these races occur together, *terrestris* averages significantly higher in numbers of gastrosteges; both have approximately same numbers of urosteges.

T. e. aquaticus differs from *T. e. terrestris* in having long, pointed snout, internasals both pointed and longer than wide, small posterior labials usually longer than tall. *Aquaticus* lacks red pigment, dorsal blotches are indistinct; *terrestris* has varying amounts of red blotching on sides and belly, often reddish-brown

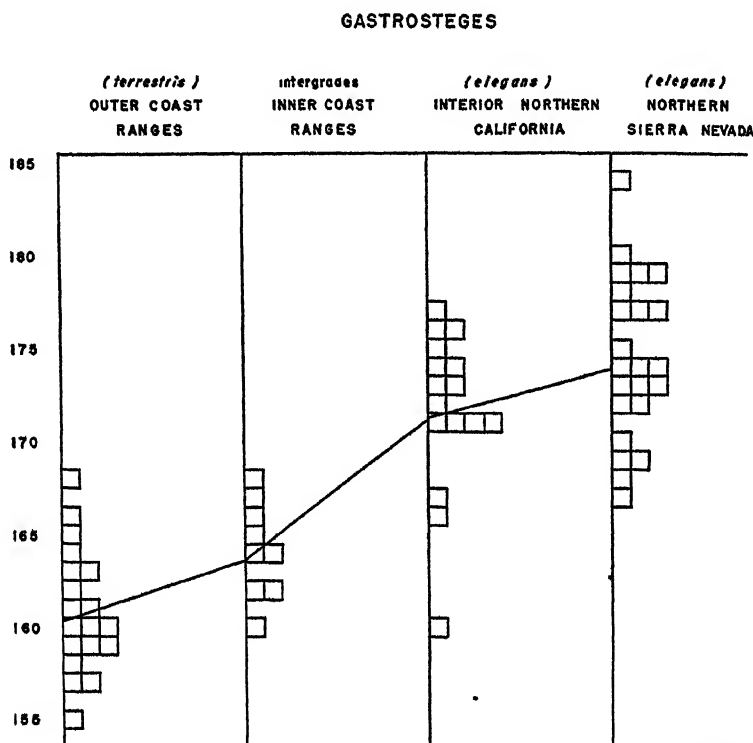


Fig. 4. Increase in numbers of gastrosteges from typical *T. e. terrestris* in coastal part of Humboldt County to typical *T. e. elegans* of Sierra Nevada by way of intergrading populations in northern inner Coast Ranges. Squares represent individual snakes; solid line connects means of samples.

ground color, characteristically distinct dorsal black blotches, no Ochraceous-Salmon suffusions on ventral scutes. Two forms similar only in pronounced dorsal stripe (usually yellow in *terrestris*, orange in *aquaticus*) and distinct lateral stripes.

T. e. terrestris and *T. e. hammondi* differ both ecologically and morphologically. In *terrestris*, internasals blunt anteriorly and shorter than broad, posterior labials enlarged; in *hammondi*, internasals pointed and longer than broad, posterior labials not enlarged. Head of *hammondi* narrower and more pointed than that of *terrestris*, eye relatively much larger. *Hammondi* has small dorsolateral blotches and no red pigment, *terrestris* large blotches and usually some red pigmentation.

Bright dorsal stripe of *terrestris* occupies $\frac{1}{2}$ -1- $\frac{1}{2}$ scale rows; completely absent or very dull and confined to neck region in *hammondi*. Divided preoculars much more frequent in *hammondi*, number of gastrosteges significantly higher.

T. e. terrestris intergrades with *T. e. elegans*, but most specimens have at least a few red spots; *elegans* has no red pigment. *Terrestris* has reddish-brown or olive-brown dorsolateral ground color with distinct dorsolateral black blotches; *elegans* has blackish ground color and indistinct black blotches. Dorsal and lateral stripes brighter in latter race, and top of head blacker, contrasting sharply with light-

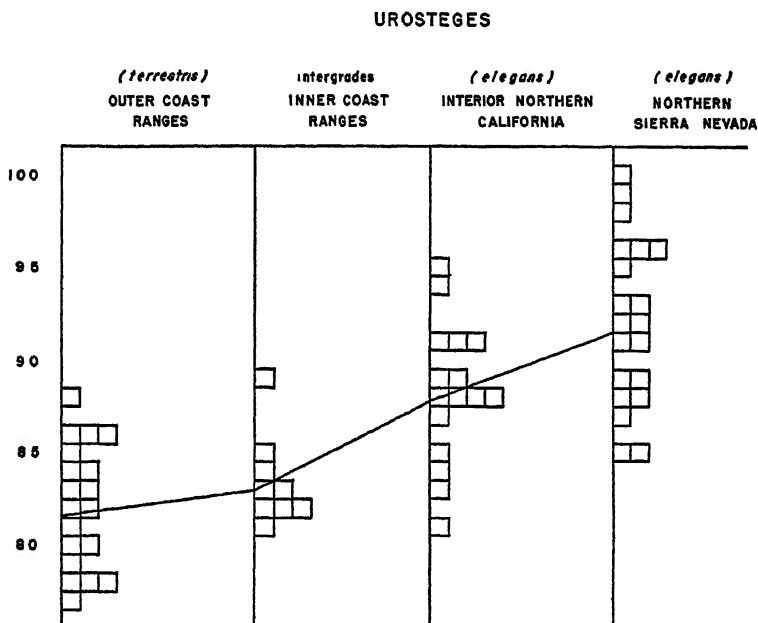


Fig. 5. Increase in numbers of urosteges from typical *T. e. terrestris* in coastal part of Humboldt County to typical *T. e. elegans* of Sierra Nevada by way of intergrading populations in northern inner Coast Ranges. Squares represent individual snakes; solid line connects means of samples.

colored labials and throat. Counts of gastrosteges and urosteges average far lower in *terrestris* (figs. 4 and 5). *Elegans* almost invariably has maximum of 21 scale rows, *terrestris* either 19 or 21.

Ranges of *T. elegans terrestris* and *T. ordinoides* overlap for a short distance (Fox, 1948). *T. ordinoides* has shorter, squarer snout and relatively smaller head less distinctly separated from neck. *Terrestris* has a fairly constant yellow dorsal stripe occupying $\frac{1}{2}$ -1- $\frac{1}{2}$ scale rows; *T. ordinoides* frequently has a broad red dorsal stripe superimposed on a narrower stripe of dull yellow. In *ordinoides* lateral stripes often absent, in *terrestris* always present and conspicuous. Maximum scale rows usually 19 or 21 in *terrestris*, most frequently 17 in *ordinoides*; former usually has 17 scale rows at posterior end of body, latter 15. Averages of gastrosteges and urosteges considerably higher in *terrestris*.

Geographic variation and relationships.—*T. e. terrestris* is uniform in certain characteristics throughout its range, but in others it is highly variable. Body and head shapes do not appear to vary appreciably, but there is considerable variation in size. The smallest specimens come from the northern part of the range, the largest are from Alameda and Contra Costa counties. Specimens from Marin County are somewhat smaller than those from the two East Bay counties; south of San Francisco Bay through Santa Cruz and Monterey counties they increase in size.

Scale characters vary somewhat erratically (tables 1 and 2; figs. 11 and 12). Specimens from Alameda and Contra Costa counties have the greatest number of ventral and caudal scutes, those from San Mateo and Marin counties have considerably lower counts, and the numbers continue to decrease through Mendocino County. Northward through Humboldt County, however, the average increases, and in Del Norte County it exceeds that of all southern localities except Alameda and Contra Costa counties. The higher counts found in *T. e. terrestris* from the north may well be due to the closer relationship with *T. e. elegans*, with which form it intergrades eastward (Fitch, 1940). Snakes in Marin County and coastal areas of Mendocino County appear to be more effectively isolated from *elegans* influence. One specimen from four miles southwest of Lakeport, Lake County, might be classified as typical *terrestris* on the basis of color; another from Kelsey Creek, Lake County, might be classified as *elegans*. Actually, both are intermediate between *terrestris* and *elegans* of northeastern California. Specimens from eastern Humboldt County, eastern Mendocino County, and western Trinity County can also be regarded as *terrestris-elegans* intergrades. They lack red pigmentation and superficially appear closer to *elegans*, but in scale counts they average only slightly higher than *terrestris* (figs. 4 and 5). There is a gradual increase in scale counts from coastal *terrestris* to the northern Sierran *elegans*. Certain specimens from the more eastern parts of the Berkeley-Oakland hills in Contra Costa County lack the red spots typical of *terrestris*. The black dorsolateral region, pronounced yellow dorsal stripe, and high scale counts of these snakes cause them to resemble *elegans* to a high degree. Since there are, however, no *elegans* near this area, the similarities must be the result of parallel evolution rather than of intergrading influences.

The color of the dorsal stripe of *terrestris* is rather bright throughout most of the range but is somewhat duller in Humboldt and Del Norte counties. Populations along the coast on both sides of the Golden Gate are characterized by a reddish-brown dorsolateral ground color between the distinct black blotches. This gives way to an almost pure black or dark olive drab eastward in the East Bay region, southward through Santa Cruz and Monterey counties, and northward through Humboldt and Del Norte counties. Snakes from the San Francisco peninsula represent the purest population of reddish-brown individuals, but individuals of that color occur in almost all parts of the range.

T. e. terrestris overlaps the range of *T. ordinoides* in northern Del Norte County without interbreeding (Fox, 1948). Its close relationship with this form cannot be denied, although each appears to be a distinct species. The two are the only forms of west coast garter snakes that have irregular red spotting over the dorsal

and ventral surfaces. Both frequently have divided preoculars and seven rather than eight upper labials. In addition, there is a certain similarity in the number of scale rows and gastrosteges and urosteges. Nonetheless the two are distinct. *T. e. terrestris* occupies part of the ranges of *T. e. hydrophila*, *T. e. aquaticus*, and *T. e. atratus* without interbreeding with them.

Ecology.—*T. e. terrestris*, according to the classification used in this paper, belongs with the terrestrial group of the *Thamnophis elegans* rassenkreis. Its ecological preferences are indicated best by its feeding habits. Stomach contents found in *T. e. terrestris* included the following items: the large slugs (*Ariolimax*) and various small gray slugs; rodents (*Microtus californicus* and *Peromyscus maniculatus*); lagomorphs (young *Sylvilagus bachmani*); plethodontid salamanders (*Batrachoseps attenuatus*, *Ensatina eschscholtzii*, *Aneides lugubris*); birds (young *Zonotrichia leucophrys*); snakes (*T. e. terrestris*); and lizards (*Sceloporus occidentalis*). Fitch (1940:96) listed in addition: *Gerrhonotus*, *Coluber constrictor*, *Spinus* sp., earthworms, fish, and fish eggs. These records could refer to either *terrestris* or *atratus* since Fitch considered *atratus* and *terrestris* as one form. Although I found no fish in the natural diet of *terrestris*, in captivity these snakes ate fish avidly, as well as *Hyla regilla* and native species of *Rana*. It is worthy of note that specimens collected in Alameda and Contra Costa counties had fed chiefly on the giant slug, whereas those from the San Francisco peninsula had fed chiefly on the meadow mouse, *Microtus*, and those from Marin County had eaten a much wider variety of food.

When Fitch (1940:95) described the ecology of *atratus* in relation to water he must certainly have been basing his observations upon *terrestris* since they do not apply at all to *atratus* as it is defined here. My observations of *terrestris* suggest that it is not dependent upon permanent water. It occasionally is found in stream beds and is abundant in riparian situations, an association probably chosen because of the overhead protection it affords. It is numerous in grassland, but usually remains within a fairly short distance of taller, denser vegetation. Open chaparral with grass is generally populated. Many small canyons with live oak (*Quercus agrifolia*), bay (*Umbellularia californica*), and numerous shrubs have large populations of this form. On flat coastal areas it is abundant along the edges of the dense growths of blackberry (*Rubus vitifolius*), thimbleberry (*Rubus parviflorus*), and *Baccharis*. Disturbed areas where dense stands of poison hemlock (*Conium maculatum*) are growing appear to be particularly favored. These observations indicate that certain aspects of the form of the plants rather than the species make them suitable for habitation by this race. These snakes seem to prefer an edge situation where they can forage for food and expose themselves to the sun, on the one hand, and on the other, escape from enemies or protect themselves from the sun when it becomes too hot. The limitation of this race to moist areas may be due to the moisture requirements of the prey species, but since *terrestris* is sharply restricted to the humid coast belt it may well have greater moisture requirements than are suggested by its habits.

Although it may be found very close to them, *T. e. terrestris* does not offer strong competition to the other members of the genus that occur with it in the San Francisco Bay region. For example, in San Mateo County I have taken *T. e. terrestris*,

T. e. atratus, and *T. sirtalis* from beneath the same piece of corrugated iron a few yards from the edge of a pond. In this particular situation, examination of the stomach contents made it clear that *atratus* and *sirtalis* were obtaining food from the pond, while *terrestris* was feeding primarily on the abundant *Microtus* in the surrounding grassland and open chaparral. Although frogs were available to *terrestris* and are known to have been eaten by this form both in the wild and in captivity, not one of the several hundred specimens of *terrestris* which I collected in the vicinity of this pond contained a frog. It might be added that in the years in which I collected in this region, the *Microtus* population was large.

Records of occurrence.—CALIFORNIA: Del Norte Co.—3 mi. N town of Smith River (MVZ 1); 3 mi. N Crescent City (MVZ 22); 100 yds. S Wilson Creek (MVZ 2); on Smith River, 3 mi. E town of Smith River (MVZ 1); Requa (MVZ 16, CAS 10); ½ mi. E Klamath, N side Klamath River (MVZ 52); Klamath Glen (WF 2). Siskiyou Co.—Klamath River at mouth Clear Creek (MVZ 1). * Humboldt Co.—Klamath River at mouth Bluff Creek (MVZ 2); * Prairie Creek State Park (MVZ 1); Prairie Creek, 2 mi. N Orick (MVZ 6); East Fork Willow Creek (MVZ 4); * Redwood Creek at Grays Resort (MVZ 1); * Trinidad (CAS 2); Eureka (MVZ 2); Elk River, 5 mi. S Eureka (MVZ 6); Fernbridge (MVZ 1); 5 mi. NE Ferndale (MVZ 1); Rohnerville (MVZ 1); Carlotta (CAS 55); 2 mi. N Orick (MVZ 5); 3 mi. W Bridgeville (MVZ 1); * Cuddabeck (MVZ 1); Bull Creek Post Office (MVZ 1); Maple Creek, 1 mi. N junction Mad River (MVZ 3); Redwood Creek, 800 ft. (MVZ 1); 8 mi. SW Dinsmore (MVZ 1); * Cobbs (MVZ 3). * Mendocino Co.—Rattlesnake Creek, 9 mi. SE Cummings (MVZ 1); * Mount Sanhedrin (CAS 1); * Fort Bragg (MVZ 6); Eagles Nest, Noyo River (MVZ 1); 3 mi. N Ornabaum Springs (MVZ 1); Garcia River, ½–10 mi. above mouth (SNIIM 1); Elk Creek, 3 mi. S Elk (MVZ 2); Elk (MVZ 73); Point Arena (MVZ 2); Mendocino City (MVZ 3); Anchor Bay (MVZ 1); 7 mi. up Navarro River (MVZ 1); Van Damme State Park, 14 mi. S Fort Bragg (MVZ 1); Gualala (MVZ 7). Lake Co.—4 mi. SW Lakeport (MVZ 1); * Kelsey Creek, Glenbrook, 4 mi. NW Cobb (WF 1). * Napa Co.—Mount St. Helena (CAS 1); St. Helena (CAS 1). Sonoma Co.—Mouth Gualala River (MVZ 3); Skaggs Springs (CAS 5); Duncan Mills (CAS 4); 7 mi. W Cazadero (MVZ 3); Freestone (MVZ 3); 2 mi. S Guerneville (MVZ 1); Montesano (MVZ 2); Jenner (MVZ 1); mouth Russian River (SNIIM 5); Austin Creek (CAS 1); Kidd Creek (CAS 1); mouth Russian Gulch, 2¾ mi. N Jenner (MVZ 1); mouth Petaluma Creek, E Black Point (MVZ 1). Marin Co.—Inverness Creek (MVZ 1); Inverness (MVZ 1); 3 mi. W Inverness (MVZ 8); Millerton Gulch, 150 ft., 2½ mi. NE Inverness (MVZ 1); 1 mi. W Point Reyes Station (CAS 4); Point Reyes Station (MVZ 1); Abbot's Lagoon (MVZ 7); Camp Taylor, Paper Mill Creek (MVZ 1); Tocaloma (CAS 5); 2 mi. W Tocaloma (MVZ 1); San Geronimo (MVZ 1); Lagunitas Creek (MVZ 1); Mill Valley (MVZ 1); west end Elk Valley (MVZ 5); Bodega Bay (MVZ 23); Clark School, Bloomfield Rd., 17 mi. W Petaluma (MVZ 1); Dillon Beach (MVZ 90); 4 mi. NNE Dillon Beach (MVZ 8); Lake Ranch, 5 mi. N Bolinas (MVZ 6); Tomales Point (MVZ 1). Solano Co.—2 mi. E Benicia (MVZ 1). Contra Costa Co.—Walnut Creek (MVZ 1); Moraga Valley (MVZ 1); Redwood Canyon (MVZ 7); 2 mi. S Lake Orinda (MVZ 1); 1 mi. E junction Walnut Creek–Moraga Rd. (MVZ 1); Wildcat Canyon (MVZ 33); Brooks Island (MVZ 1); Las Trampas Creek, St. Mary's College (MVZ 3). Alameda Co.—Vicinity Berkeley (MVZ 47); San Leandro (MVZ 1); Thornhill Pond (MVZ 2); Airport Rd., East Oakland (MVZ 1); Oakland (MVZ 1); Claremont Canyon (MVZ 10). San Francisco Co.—(MVZ 91); Goat (Yerba Buena) Island, San Francisco Bay (MVZ 3). San Mateo Co.—Skyline Blvd., 8–6 mi. S San Francisco Co. line (MVZ 244); San Andreas Lake (SNHM 8); Skylanda (SNHM 1); Eisenberg Ranch, Skyline Blvd., S La Honda Rd. (SNHM 1); Menlo Park (SNHM 2); Sharp Park (MVZ 38); Rockaway Beach (MVZ 2); Montara (MVZ 1); Moss Beach (MVZ 6); 2 mi. (MVZ 23), 8.1 mi. (MVZ 4), 4.5 mi. (MVZ 3), and 5.8 mi. (MVZ 1) S Half Moon Bay; San Gregorio Creek (MVZ 4); Pescadero Creek (MVZ 6). Santa Clara Co.—Alma (MVZ 1); San Jose (CAS 1); Palo Alto (SNHM 10); Stevens Creek (SNHM 1); 12 mi. from summit Mount Hamilton toward Livermore (SNHM 1). Santa Cruz Co.—Soquel (SNHM 4); Felton (SNHM 1); Glenwood (CAS 1); Boulder Creek (MVZ 1); 3 mi. E Santa Cruz (MVZ 2); Santa Cruz

* Intergrades.

(MVZ 2); mouth Scott Creek, 1 mi. NE Jarro Point (MVZ 1). *Monterey Co.*—Elkhorn Slough (SNHM 2); Carmel (CAS 4, MVZ 1); N side Carmel Valley, off U. S. 101 (SNHM 1); 1 mi. E mouth Carmel River (MVZ 1); Garrapatas Creek (SNHM 1); Parkington Canyon (SNHM 1); Mill Creek (SNHM 2); Pacific Grove (SNHM 7, MVZ 1); Pajaro River (MVZ 1); Big Pines (MVZ 2); north gate 17-Mile Drive (MVZ 1); mouth Little Sur River (MVZ 2, SNHM 2). *San Luis Obispo Co.*—Oceano (CAS 1); Morro Rock (MVZ 1); Morro (CAS 1). *Santa Barbara Co.*—Santa Ynez River (MVZ 1); Santa Barbara (SBNHM 1).

DISCUSSION

A full review of the members of the *Thamnophis elegans* rassenkreis has led the author to the conclusion that this complex of snakes segregates rather clearly into two ecological groups. This concept differs slightly from the interpretation of Fitch (1940), who divided the complex into three groups. The terrestrial and aquatic groups into which I have divided the rassenkreis correspond, in part, to the *Ordinoides* and *Hydrophila* groups of Fitch. His *Elegans* group, including the races *elegans*, *hueyi*, *vagrans*, and *biscutatus*, can be eliminated. I regard this group as an unnatural and unnecessary assemblage. It is justified to the extent that these races are related through intergradation, and that one race, *vagrans*, is unspecialized in its ecology and another, *elegans*, is perhaps generalized in its habits in a small part of its range. However, these reasons do not seem to me sufficient basis for placing *elegans* in a different group from *terrestris* (regarded as *atratus* by Fitch). The two forms intergrade and have a strong morphological and ecological similarity. *Hueyi* appears to be a weakly differentiated population of *elegans* and consequently should also be placed in the same group as *terrestris*. Although *biscutatus* is intermediate between *hydrophila* and *elegans* in most morphological characters, in certain respects it appears morphologically closer to the terrestrial group. However, since it is entirely aquatic in its habits (Fitch, 1940:30), I have somewhat arbitrarily placed it in the aquatic group. Ecologically speaking, *vagrans* does not fit perfectly into either group, but since it appears most closely related to *elegans* it is not out of place in the terrestrial group. Other reasons for placing *vagrans* with the terrestrial rather than with the aquatic races are that it is geographically complementary to the other terrestrial races and that it occurs without interbreeding in the same area as *couchii*, a member of the aquatic group.

The sympatric and allopatric relationships of the various races also favor division of the rassenkreis into two groups. As shown by figures 6 and 7, both the aquatic and terrestrial groups present the appearance of a polytypic species composed of several allopatric races. In addition, it is clear that the two groups are largely sympatric to each other.

The sympatric relationships of various races of this complex of garter snakes have been the basis for much criticism of the taxonomy (Mayr, 1942; Johnson, 1947). To many systematists it seems unnatural that there should be so many instances of range overlap within a single species. Prior to the demonstration of the specific status of *ordinoides* (Fox, 1948) the situation was even more complicated. When *ordinoides* was considered a subspecies, there were present in parts of Oregon and Washington three forms that were considered to be subspecies of the same species. Under the present grouping there are only two subspecies occupying the same area except in the coastal parts of Monterey and San Luis Obispo counties, where three are reported to occur (*atratus*, *terrestris*, and *hammondi*).

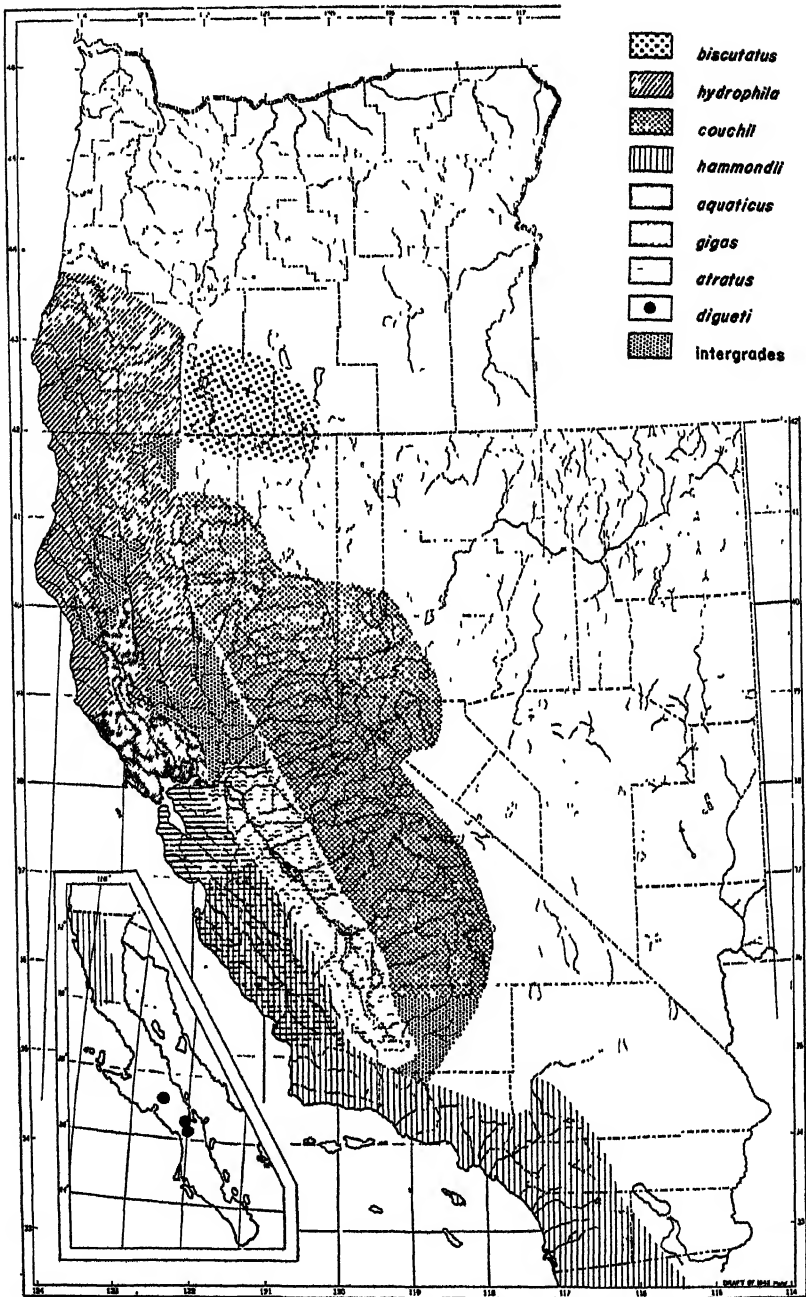


Fig. 6. Distribution of races of aquatic group of *T. elegans rassenkreis*. Races replace each other geographically, except that ranges of *T. e. atratus* and *T. e. hammondii* overlap in Monterey and San Luis Obispo counties. Note that *bisectatus* is isolated except for small area of intergradation with *hydrophila* in part of Klamath River system.

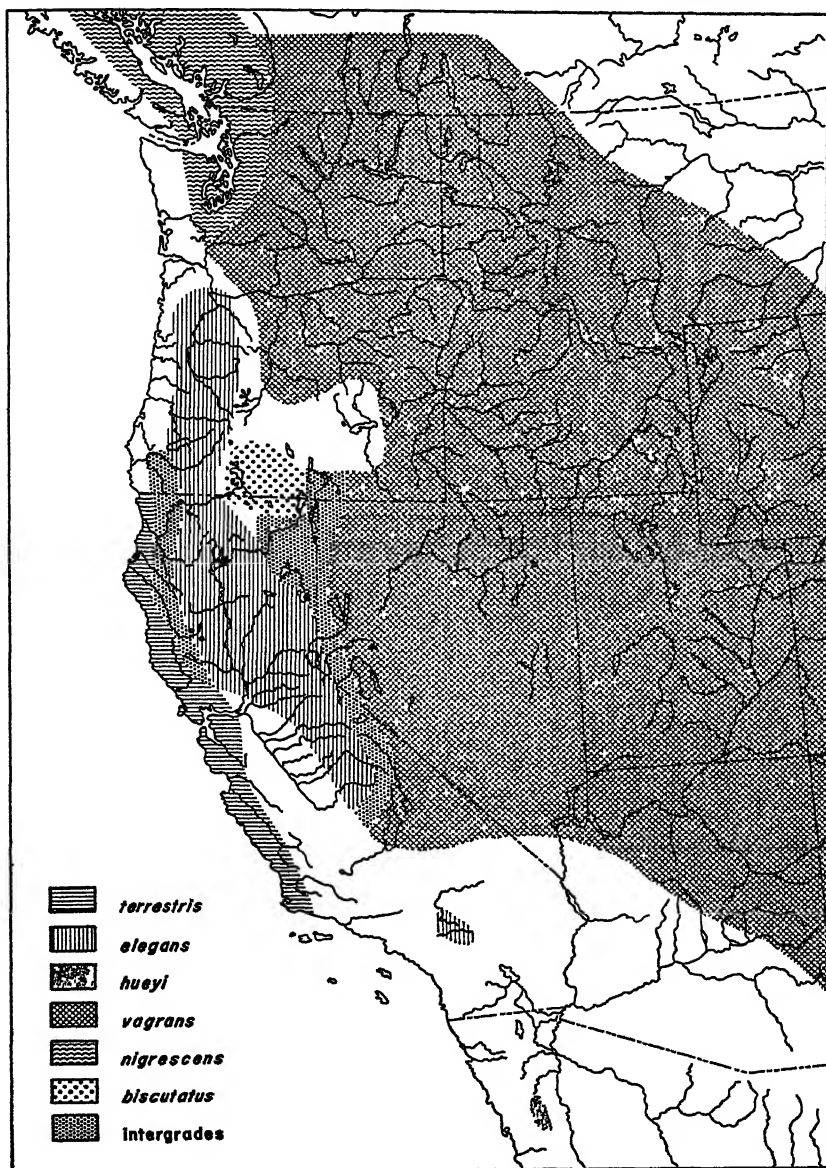


Fig. 7. Distribution of races belonging to terrestrial group of *T. elegans* rassenkreis. Races replace each other geographically. *T. e. biscutatus* of aquatic group included here to show intergradation with *elegans* and *vagrans*. Comparison of figs. 6 and 7 shows that, aside from *nigrescens*, *biscutatus* is the only race with a range not occupied, or partly occupied, by another race of the species.

The first question to be answered when considering this problem of range overlap is whether such a situation is necessarily an improbable one. Mayr (1942:180-185) has reviewed the literature and presents many instances involving chains of subspecies in which the terminal populations overlap without interbreeding. Fitch (1948:125) has also discussed this aspect of evolution and its application to the taxonomy of the garter snakes. Without reviewing the literature again, it seems sufficient to state that the problem of range overlap among the garter snakes differs in no critical respects from that involved in the instances cited by Mayr (*loc. cit.*), except that the degree of overlap is much more extensive than in other known cases. However, the degree of morphological and ecological differentiation is far greater than in the usual picture of geographic variation, a condition which suggests that physiological or psychological barriers to interbreeding may develop more readily in these snakes than in most other terrestrial vertebrates.

The second question which must be answered in evaluating the significance of this complex is whether it is possible that, between one race and another, some special type of intergradation occurs which might entail a barrier to gene flow. Is Fitch correct in describing smooth intergradation between the critical races that involves transition from aquatic to terrestrial ecology? Originally the scope of this study did not include this problem and I attempted no new field work in the critical regions of intergradation. However, the specimens upon which Fitch based his conclusions are in the Museum of Vertebrate Zoology of the University of California, and I have carefully reexamined them.

Fitch (1940:54-55) described smooth intergradation between *hydrophila* and *biscutatus* up the Klamath River drainage (fig. 13). Both races are aquatic in habits, but *biscutatus* possesses somewhat enlarged supralabials and internasals which are less pointed than those of *hydrophila*. Specimens from near the mouth of the Klamath River are typical *hydrophila* but have a slightly increased tendency for divided preoculars, a character particularly common in *biscutatus*. Eastward, through the Klamath drainage, the snakes encountered gradually become more typical of *biscutatus* until pure *biscutatus* is found in the upper drainage of the Klamath River. *Biscutatus* appears to be isolated from *hydrophila* of the Rogue River basin to the west by the Cascade Range (Fitch, 1940:29). It appears to be further cut off to the north by the abrupt rise of a high, arid plateau (fig. 6).

East of the Klamath drainage in the Warner Lakes basin *biscutatus* intergrades with *vagrans*. In the Warner Mountains the garter snakes appear to be a composite of *biscutatus*, *vagrans*, and *elegans* (fig. 7). In northern Lassen County specimens of *elegans* vary considerably from typical members of this race and indicate intergradation with *biscutatus* in all characters. These specimens approach the maximum adult size of *biscutatus* rather than that of *elegans*; the dorsal ground color is not the glossy black of *elegans*; the dorsal stripe is not as bright as that of *elegans*; the body proportions, head shape, muzzle proportions, internasals, genials, numbers of ventrals and caudals all resemble *biscutatus* or are intermediate between the two races.

. In reexamining the material from which Fitch described the above-mentioned intergradations I was very critical. However, I can only report that I found the evidence, based on many specimens from the critical areas, to be exactly as repre-

sented by Fitch. I see no alternative, unless new information is brought to light, to acceptance of the conclusion that all the subspecies of the *Thamnophis elegans* rassenkreis are connected by intergrading populations. At no point is there justifi-

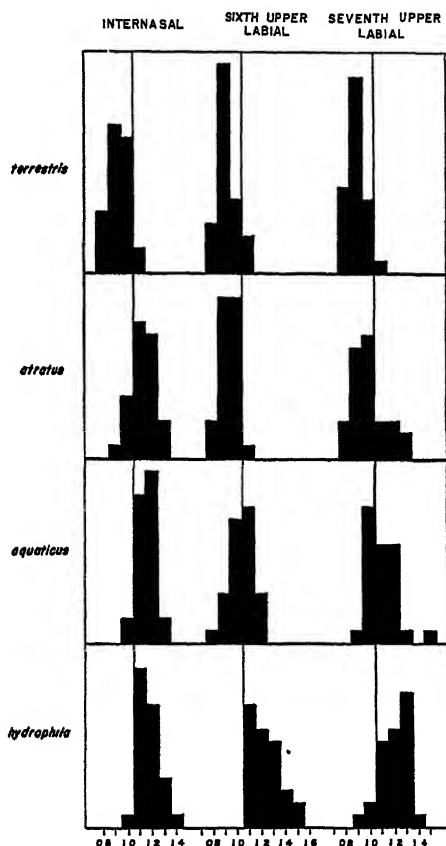


Fig. 8. Variation in proportions of internasals and sixth and seventh upper labials in aquatic and terrestrial races. Scale shows ratios of length divided by width for internasals, length divided by height for upper labials. Vertical line running through graphs of internasals separates individuals with internasals as broad or broader than long (on the left) from those with internasals longer than broad (on the right). Individuals with taller upper labials are left of vertical lines. Figures based on 80 individuals of each race.

cation for drawing lines through these intergrading populations in order to set up categories at the species level.

THE AQUATIC GROUP

The aquatic group is composed of eight forms of garter snakes that are mainly dependent upon aquatic or amphibious prey for food and are usually dependent upon the presence of some body of water into which they can retreat from preda-

tors. Certain morphological and behavioristic tendencies occur throughout this entire group in spite of considerable geographic variation.

The snakes in this group have relatively long, narrow, pointed heads and a relatively long gape (fig. 9). Their internasals are usually pointed and longer than broad (fig. 8). Bright colors are extremely rare. Red pigment is known to occur only in a few individuals of the intergrading population of *aquaticus* and

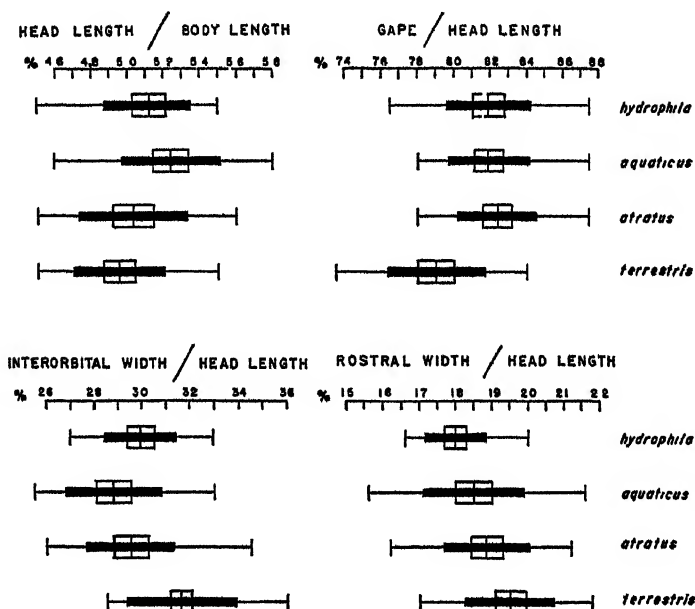


Fig. 9. Variation in head proportions of aquatic and terrestrial races. Head length in terms of percentages of body length; length of gape in terms of percentages of head length. Interorbital width and rostral width of head presented in terms of percentages of head length. Range of variation within each population represented by narrow horizontal line ending in terminal bars. Solid horizontal bar represents standard deviation plotted on both sides of mean; open rectangle represents twice standard error of mean plotted on both sides of mean (indicated by the short, central, vertical line). Differences between samples significant if open rectangles do not overlap (Dice and Leraas, 1936). Each sample composed of 30 individuals.

hydrophila from the South Fork of the Eel River. In all races except *atratus* and *biscutatus*, the sixth and seventh supralabials are reduced, their length being greater than their height (fig. 8). There is a tendency toward a gray or drab-colored iris among most races. Other characters show considerable variation from race to race. Observations have shown that the natural food items of this group are fish, frogs, toads, tadpoles, salamanders, and fish eggs; the snakes responded only to this specialized diet in captivity. Their initial recognition of food in captivity appeared to be chiefly through the olfactory sense. After the food was taken into the mouth, other senses seemed to be involved. For example, *T. e. couchii* could not be induced to feed on baby rats until the rats had been coated with fish oil. Apparently the odor of the fish was sufficient to induce a snake to take the rat into its mouth. Some

individuals released the oiled rats immediately after taking them into the mouth as though they had suddenly experienced an unpleasant sensation.

Evidence of the role that vision plays in the feeding habits was seen in the attentive, searching behavior that snakes frequently displayed when the water in their water dish was splashed. They apparently sought live tadpoles and fish in the water dish by sight, although they were probably first aroused by olfactory stimuli.

Another pattern of behavior that appears to be of more frequent occurrence in the aquatic group than in the terrestrial group is the flattening of the body and head and partial raising of the body from the ground in a striking coil. *Thamnophis sirtalis* also frequently behaves in this manner.

GEOGRAPHIC VARIATION IN THE AQUATIC GROUP

Variation in the dorsal stripe.—In the aquatic group the dorsal stripe is broad in the subspecies *atratus*, *aquaticus*, and *biscutatus*. In these races it occupies at least $\frac{1}{2}$ -1- $\frac{1}{2}$ scale rows. Fitch (1940: 83, 103) has suggested that the broad dorsal stripe is characteristic of terrestrial garter snakes and that it might have a protective value for forms that occur in dense vegetation, whereas a broad dorsal stripe might render snakes among rocks in open streams more conspicuous to predators. It is of interest to determine whether the aquatic races that have a broad dorsal stripe support these generalizations. *Biscutatus* occurs in an area abounding in lakes, although Fitch claims to have found it chiefly in rocky streams. The presence of a broad dorsal stripe in this subspecies, however, may be influenced partly by intergradation with *elegans*. *T. e. atratus*, on the other hand, occurs in an area where there are very few large streams, and it chiefly inhabits ponds and small streams. *T. e. aquaticus* likewise has access only to small streams and ponds in part of its range; in other parts there are slow, muddy streams. It inhabits swift, rocky streams only in the most northern part of its range where it intergrades with *hydrophila*, a form with a reduced dorsal stripe.

It is possible that in the habitat situations which have been described the snakes may be dependent upon the surrounding vegetation for escape and concealment, rather than upon the water and the rocks. As pointed out, *atratus* appears to be much less dependent upon large bodies of water than any of the other aquatic races are. Both *aquaticus* from the southern part of its range and *atratus* are frequently captured in grass or grass-brush situations in the vicinity of bodies of water. A correlation between the presence of a broad dorsal stripe and a more terrestrial habitat is thus borne out to a large extent.

Variation in dorsolateral color.—The dorsolateral ground color of races of the aquatic group is never bright, but olive grays and olive browns predominate. Very dark, olive-drab shades are characteristic of *atratus*, *aquaticus*, and *biscutatus*. In coastal *hydrophila* the ground color is olive brown, in *hydrophila* of the interior olive gray. Various shades of brown and gray are characteristic of the other races. The dorsolateral black blotches, characteristic of many races, are for the most part indistinct in *atratus*, *aquaticus*, and *biscutatus*. There is considerable variation in the size of the blotches in the few *atratus* in which they are discernible, but I have been unable to detect any consistent trends. Typical *hydrophila* has large dorsolateral blotches which give it a checkered appearance; but in the coastal *hydrophila*

these blotches are usually very small. In *couchii* the blotches are large and appear to overlap at the corners. Both *gigas* and *hammondi* have well-segregated blotches which are smaller than those of *couchii*; in *digueti* the blotches are extremely small.

Variation in the proportions of parts of the head.—The aquatic group has been described earlier as having a relatively longer head, longer gape, longer, pointed internasals, and smaller but relatively longer posterior supralabials than the terrestrial group (figs. 8 and 9). The races *atratus* and *biscutatus* have been found to approach the terrestrial group in several of these characters. *Atratus* appears to be intermediate between *hydrophila* and *terrestris* in head length and in rostral width (fig. 9). Both *atratus* and *biscutatus* possess enlarged, high posterior supralabials. It seems reasonable to postulate that many of the characteristics of *biscutatus* can be explained by its intermediate position between *hydrophila* and *elegans*. However, *atratus* cannot be explained in this manner. The shortening of the head and the increase in size of the supralabials are very probably correlated with the adoption of more terrestrial habits. Fitch (1940:16, 83) suggested that the size of the supralabials reflects the size of the salivary glands and, further, that the larger salivary glands of terrestrial forms are an adaptation for the swallowing of dry food or of food out of the water. Although *atratus* does feed on land as well as in the water, the amphibians which form its diet can scarcely be considered dry food. One wonders whether the large salivary glands of this form might not play some role in counteracting the mucus and toxins exuded by the sticky epidermis of its prey.

Variation in body size.—No statistical analysis of relative thickness of body has been attempted in this study. Adult body size varies considerably within each race, particularly among the three coastal races: *atratus*, *aquaticus*, and *hydrophila*. Coastal populations of these races mature at a smaller size than do interior populations of the same race. The population of *aquaticus* at Dillon Beach, Marin County, matures when about three-fourths the size of specimens of the same race in Napa County; the adult snakes of the Dillon Beach population seem to be smaller than in any other group of the entire species. Of 45 snakes collected there, the body length of the largest was only 437 mm. The most obvious explanation for the small size of individuals of the coastal populations is a slower growth rate of poikilothermic animals in the cool fog belt along the coast. On the other hand, there may be selective value for smaller size in coastal populations, in accordance with the studies of surface-volume ratios which have led to the general rule that poikilothermic animals tend to be smaller in cooler regions. A third possible explanation involves differential growth rates. I have found that in these snakes there is fairly rapid growth during the first few years and that at maturity the rate of growth declines considerably. This has apparently been found to be true of many other snakes. Although there is a continual slow growth throughout the life span, each species has a characteristic size range, and growth rates seem to decrease appreciably at maturity. Work in progress on the growth and reproduction of garter snakes indicates that maturity is correlated with age rather than with size. Conceivably, coastal snakes deprived of optimum growing conditions might reach maturity while yet small. After this stage is reached they would be capable of growing only at the slow adult rate. This would result in a population of small snakes.

Variation in eye color.—The data on eye color are not adequate to serve as a basis for positive statements about the geographic distribution of this characteristic throughout the group. Some generalizations may be noted. Gray and drab-colored eyes with no bright ring round the pupil are typical of most aquatic races. Fitch (1940) states that both brown and gray eyes are found in *hydrophila*. In the southern part of its range, *hydrophila*, judging from the live specimens I have examined, has brown eyes. Many *hydrophila-aquaticus* intergrades and also some rather typical specimens of *aquaticus* near the area of intergradation have brown eyes. Gray eyes are typical for the remainder of the populations of *aquaticus*. *Aquaticus* near the area of intergradation with *atratus* may have dark, cloudy regions in the iris. *Atratus* has a rather dark, dusky iris, but most specimens have a light-yellow ring around the pupil. It is interesting that in these characters, as in others, *atratus* resembles *bisculatus*.

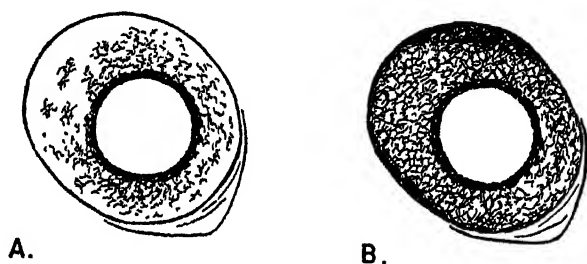


Fig. 10. Sketches of iris of *T. e. atratus* (A) and *T. e. aquaticus* (B), showing sparse silvery network of dark, dusky iris of former and dense silvery network of gray iris of latter. Underlying melanins and lipochromes not indicated.

Examination of the eyes, either with a dissecting microscope or with an Ultrapac microscope, reveals an apparently superficial silvery network over the iris. In the dark, dusky eyes this network is very loose and the underlying melanin is conspicuous. In the gray eyes this silvery network is tighter and masks some of the melanin (fig. 10). In certain of the gray eyes, light areas of lipochrome also appear to be present. The brown eye appears to be very similar to the gray, but the silvery net is even tighter and the lipochrome predominates over the melanin.

Variation in scutellation.—The snakes of the aquatic group show a fairly regular reduction in the number of gastrosteges and urosteges from the northern to the southern parts of their range (figs. 11 and 12). In general, interior populations tend to have higher scale counts than coastal populations have. Within individual samples, such as that from the tributaries of the Eel River, the specimens from the more interior localities have significantly higher numbers of gastrosteges and urosteges.

It is worthy of note (figs. 11 and 12) that the variations of gastrosteges and urosteges almost coincide. The gastrosteges show the greater variation and yield the more significant differences between the means. There is a highly significant geographic variation in these characters within each subspecies; for example, in *hydrophila*, snakes from coastal areas of Humboldt and Mendocino counties have

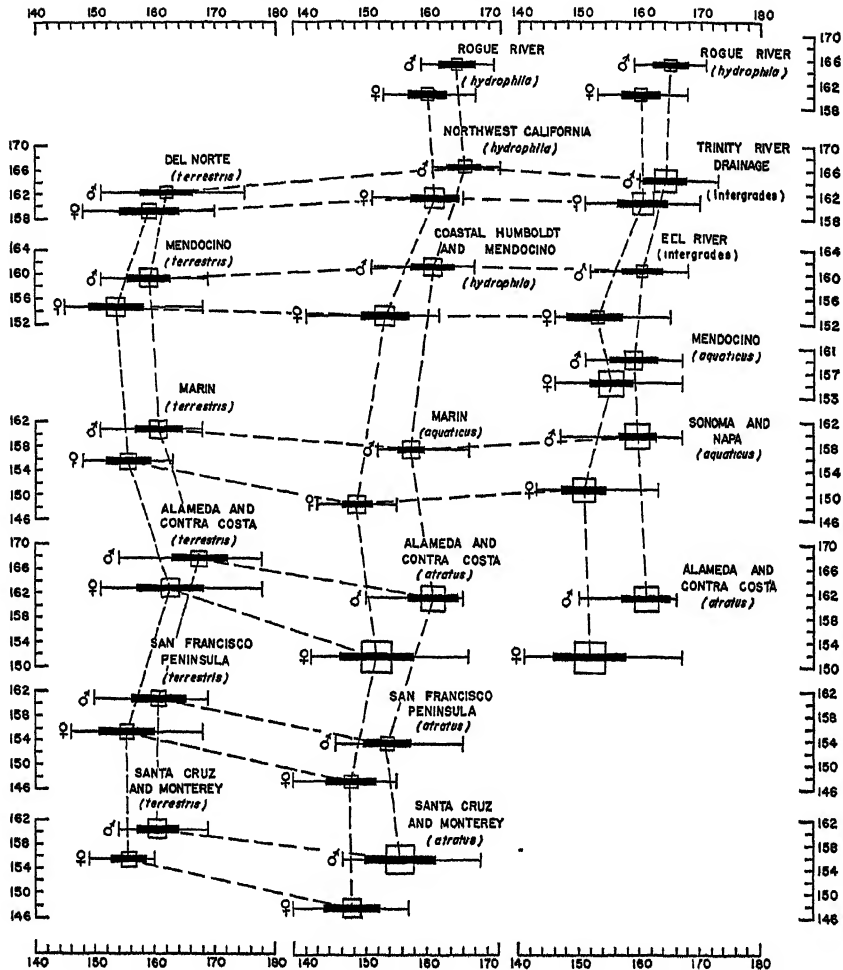


Fig. 11. Variation in numbers of gastrosteges in populations of *Thamnophis elegans* from western California and southwestern Oregon. Localities arranged from north to south. Column on left represents *T. e. terrestris*, only member of terrestrial group analyzed in detail; middle column coastal populations of aquatic group; column on right interior populations of aquatic group. Aquatic samples from Rogue River and from Alameda and Contra Costa counties represented in both middle and right-hand columns to allow comparisons with both coastal and interior samples.

In each symbol the range is indicated by the fine horizontal line between the short, vertical terminal bars; the solid bar represents the standard deviation plotted on both sides of the mean; the open square represents twice the standard error of the mean plotted both horizontally and vertically from the mean. Because there is a highly significant sexual dimorphism in numbers of gastrosteges, the sexes are plotted separately.

The graph is designed to allow comparison of samples in both the vertical columns or the horizontal rows. Samples falling within a single column or within a single row are plotted on the same scale. Broken lines connect means of samples which are to be compared. If the hollow squares do not overlap, the difference between the samples is significant (Dice and Leraas, 1936). For example: reading down the vertical column on the left reveals that both male and female *terrestris* from the Alameda and Contra Costa sample have significantly more gastrosteges than any of the other samples of *terrestris*; likewise, reading across the third horizontal row from the bottom indicates that they also have significantly more gastrosteges than *atratu* from the same locality. The numbers of individuals upon which these figures are based are recorded by localities in table 1.

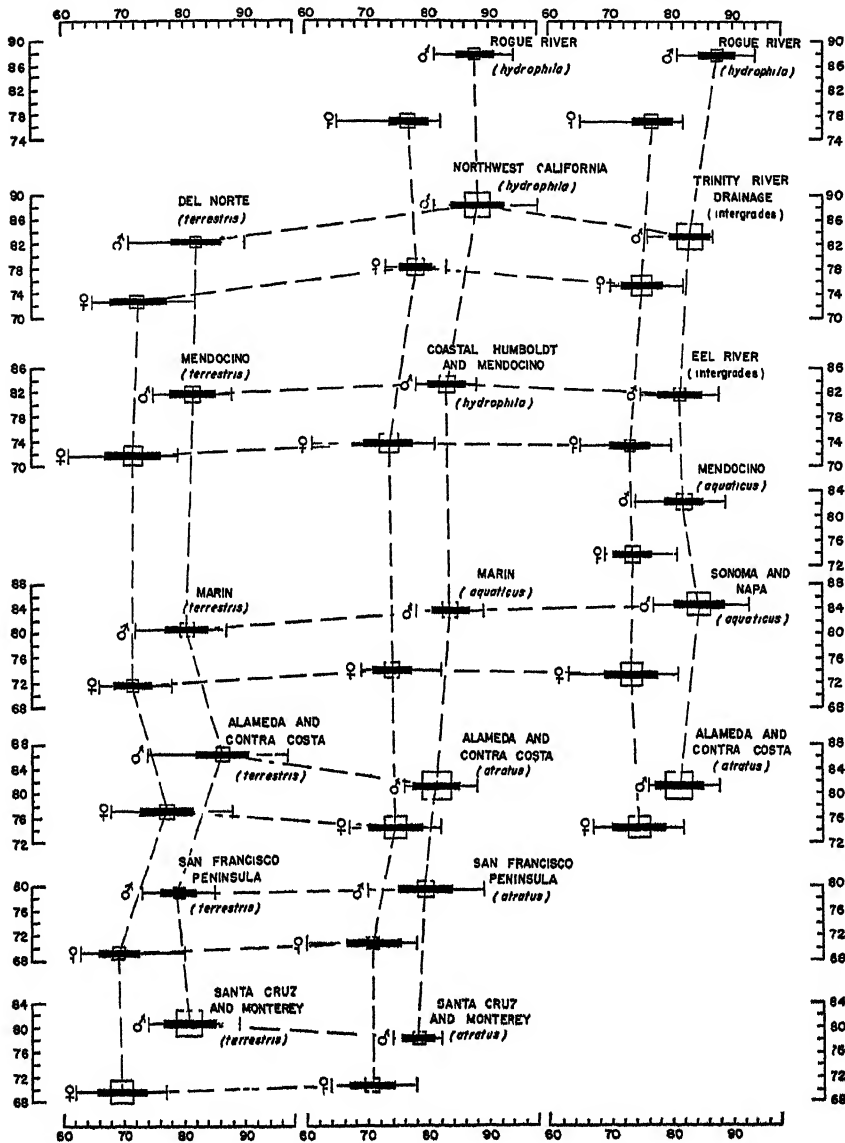


Fig. 12. Variation in numbers of urosteges in populations of *Thamnophis elegans* from western California and southwestern Oregon. For explanation of symbols see legend of fig. 11.

considerably lower average scale counts of gastrosteges and urosteges than do those from the Rogue or Lower Klamath rivers. Similarly, the average numbers of these scutes are higher in *atratu* from Contra Costa and Alameda counties than they are in *atratu* from the San Francisco peninsula.

Recognition of the three aquatic races, *atratu*, *aquaticus*, and *hydrophila*, is primarily based on color and pattern. As shown in figures 11 and 12, variations in

TABLE 1
PERCENTAGE FREQUENCIES OF SCALE ROWS

Sample	Number of snakes	Neck					Thoracic region					Posterior end of body		
		17	18	19	20	21	17	18	19	20	21	15	16	17
<i>terrestris</i>														
Del Norte Co. *	160	3.8	3.1	90.6	0.6	1.9	3.8	89.3	2.5	4.4	22.5	4.4	73.1
Humboldt Co.....	35	85.7	14.3	94.3	5.7	20.0	80.0
Mendocino Co.....	73	5.5	93.2	1.3	80.8	1.4	17.8	9.6	4.1	86.3
Marin Co.....	80	90.0	10.0	56.3	1.2	42.5	1.3	98.7
Alameda and Contra Costa cos.....	113	79.6	2.7	17.7	26.5	2.7	70.8	6.2	1.8	92.0
San Francisco peninsula.	112	89.3	2.7	8.0	24.1	4.5	71.4	2.7	1.8	95.5
Santa Cruz and Monterey cos.....	50	64.0	4.0	32.0	24.0	6.0	70.0	2.0	98.0
<i>hydropitila</i>														
Rogue River basin.....	66	19.7	80.3	65.2	34.8	16.7	1.5	81.8
Northwest California....	43	39.5	60.5	41.9	4.6	53.5	20.9	79.1
Coastal Humboldt and Mendocino cos.....	48	95.8	4.2	97.9	2.1	68.8	8.3	22.9
<i>intergrades</i>														
Trinity basin.....	44	93.2	2.3	4.5	88.6	4.6	6.8	52.3	2.2	45.5
Eel River basin.	131	100.0	100.0	74.8	3.8	21.4
<i>aquaticus</i>														
Mendocino Co.....	52	98.1	1.9	94.2	1.9	3.9	63.5	11.5	25.0
Sonoma and Napa cos.....	59	94.9	1.7	3.4	96.6	3.4	50.8	6.8	42.4
Marin Co.....	51	100.0	2.0	98.0	82.4	11.8	5.8
<i>atratus</i>														
Alameda and Contra Costa cos.....	39	97.4	2.6	97.4	2.6	81.5	4.0	14.5
San Francisco peninsula.	114	2.6	97.4	100.0	92.3	7.7
Santa Cruz and Monterey cos.....	66	1.5	97.0	1.5	100.0	84.8	3.1	12.1

* Localities are listed from north to south.

TABLE 2
AVERAGE PERCENTAGE FREQUENCIES

Sample	Number of snakes	Supralabials						Infralabials						Preoculars		Postoculars			
		6	7	8	9	7	8	9	10	11	12	1	2	1	2	3	4		
<i>terrestris</i>																			
Del Norte Co. *	153	2.8	23.8	63.0	0.4	0.3	6.0	42.4	51.3	95.9	4.1	0.3	12.7	85.8	1.2		
Humboldt Co.....	36	1.4	25.0	73.6	8.3	29.2	61.1	1.4	88.9	11.1	11.8	88.2		
Mendocino Co.....	73	14.7	86.3	21.2	78.8	96.6	3.4	8.2	87.0	4.8		
Marin Co.....	80	7.5	92.5	0.6	17.5	79.4	2.5	87.5	12.5	8.1	90.0	1.9		
Alameda and Contra Costa cos..	150	1.2	3.2	95.6	0.5	10.6	88.9	85.4	14.6	4.0	94.9	1.1		
San Francisco peninsula.....	112	0.9	5.8	93.3	1.4	16.9	81.7	94.2	5.8	100.0		
Santa Cruz and Monterey cos....	50	1.0	99.0	6.0	94.0	96.0	4.0	3.0	93.0	4.0		
<i>hydrophila</i>																			
Rogue River basin.....	96	1.6	97.9	0.5	6.8	89.1	3.6	0.5	91.1	8.9		
Northwest California.....	44	4.5	95.5	1.1	1.1	8.0	89.8	78.4	21.6		
Coastal Humboldt and Mendocino cos.....	48	5.2	94.8	1.0	6.3	91.7	1.0	100.0		
<i>intergrades</i>																			
Trinity basin.....	44	1.1	96.6	2.3	4.5	86.4	9.1	100.0	97.7	2.3		
Eel River basin.....	106	2.8	96.2	1.0	0.9	13.7	84.0	1.4	99.1	0.9	1.4	96.2	2.4		
<i>aquaticus</i>																			
Mendocino Co.....	48	4.2	93.8	2.0	11.5	85.4	3.1	100.0	2.1	91.6	6.3		
Sonoma and Napa cos.....	59	1.7	98.3	14.4	83.1	2.5	99.2	0.8	2.5	96.7	0.8		
Marin Co.....	51	100.0	1.0	21.6	72.5	4.9	100.0	7.8	92.2		
<i>abstratus</i>																			
Alameda and Contra Costa cos..	42	98.8	1.2	1.1	3.6	91.7	3.6	95.2	4.8	1.2	98.8		
San Francisco peninsula.....	114	1.8	97.8	0.4	8.8	90.8	0.4	93.4	6.6	5.4	94.6		
Santa Cruz and Monterey cos....	66	3.8	95.5	0.7	6.8	90.9	2.3	93.2	6.8	3.8	92.4	3.8		

the number of ventral and caudal scutes are sometimes greater between populations within the subspecies than they are between the subspecies themselves. Because of the wide variation within each population, these characters are of little value in recognition of the subspecies. Averages for *altratus* are slightly lower than those for *aquaticus*, but these differences are not significant. Both *altratus* and *aquaticus* have significantly lower scale counts than most populations of *hydrophila* have.

Table 1 shows the variation in numbers of scale rows around the body. This character also exhibits a fairly consistent cline in the aquatic group. The largest number of scale rows—21 at the neck, 21 at the thoracic region, and 17 at the posterior end of the body—is most characteristic of *hydrophila*. However, specimens of this subspecies from coastal areas of Humboldt and Mendocino counties show a very pronounced decrease in the number of scale rows. *Aquaticus* characteristically has 19 scale rows at the thoracic region. Although there is a strong tendency for it to have 15 scale rows at the posterior end of the body, specimens with 16 or 17 appear in significant numbers. *Altratus* rarely varies from 19 scale rows at the neck and thoracic regions. Fifteen are usually present at the posterior end of the body, but 16 and 17 occur in a small number of specimens.

Numbers of supralabials, infralabials, and preoculars have no value in identification of *hydrophila*, *aquaticus*, or *altratus* (table 2). Although some populations show more variation than others in respect to these characters, there are no consistent trends.

For details of variation in *biscutatus*, *couchii*, and *hammondii* see Fitch (1940).

THE TERRESTRIAL GROUP

The terrestrial group is composed of races that are known to feed largely or entirely on terrestrial animals and that are not regularly dependent upon bodies of water as a refuge from their enemies. Certain morphological characteristics are common to the entire group. There is a conspicuous, broad dorsal stripe (except in *vagrans*, in which it is frequently inconspicuous); the internasals are as broad, or broader, than they are long and usually are not sharply pointed; the sixth and seventh supralabials are taller than they are long and are generally enlarged (fig. 8). The outstanding geographic trends within the group primarily involve the ground color, the conspicuousness of the dorsal stripe, and scutellation. The five races included in this group are geographically complementary and intergrade with each other at points of contact.

Thamnophis ordinoides has the morphological and ecological characteristics of this group, but because of its sympatric relationship with several of the other races, it is questionable whether it should be included in this complex. Fitch (1940:93) and Fox (1948) demonstrated the very close morphological and ecological similarity of *T. ordinoides* and *T. e. terrestris* (designated by them as *altratus*). There seems to be little reason to doubt that these were once intergrading populations that became geographically isolated and upon renewal of contact failed to interbreed.

Fitch (1940:20) described a population of *vagrans* from British Columbia which differed from typical *vagrans* in the gastrosteges, urosteges, preoculars,

dorsolateral ground color, dorsolateral blotches, ventral pigmentation, and head shape. He recognized that the area occupied by this population was faunally distinct from the rest of the range of *vagrans*. However, he did not consider the differentiation to be sufficiently marked to warrant the establishment of a distinct subspecies.

Johnson (1947) described this population as *T. e. nigrescens* and emphasized its distinctness from typical *vagrans*. Fitch (1948:123) reviewed this situation and reiterated his original opinion that the differentiation was not on a subspecific level. Fitch stated that since the degree of differentiation of this population is far below that exhibited by the established subspecies, recognition of it as a subspecies is inconsistent. I go even farther and state that, except for the race *hueyi*, the differences between subspecies of *T. elegans* are of a different character than those exhibited by *nigrescens*. The differences that exist between *hueyi* and *elegans* and between *nigrescens* and *vagrans*, however, are typical of the kind of average variations that exist between ordinary geographic races of other vertebrate species. For this reason I feel that it is desirable to grant them subspecific status. Unfortunately, the use of the trinomial completely fails to express the true relationships. For *hueyi* or *nigrescens* a quadrinomial (e.g., *Thamnophis elegans vagrans nigrescens*) might be used to clarify its position in the rassenkreis. This scheme would not be satisfactory for most of the other interrelated races, however, since the degree of differentiation among them varies considerably.

Although it is clear that neither *hueyi* nor *nigrescens* will fit easily into the present scheme of classification, I believe that it is worth while to name such distinct populations. I feel that it is simplest to accept both as valid subspecies, even though such classification introduces certain inconsistencies into the present concept of subspecific differentiation within the group. I want it understood, however, that I agree thoroughly with Fitch that the claim of *nigrescens* to subspecific distinction is relatively weak. My suggestion should in no way be construed as an attempt to encourage the splitting of the major subspecies of the rassenkreis into their many small microgeographic populations.

GEOGRAPHIC VARIATION IN THE TERRESTRIAL GROUP

Variation in the dorsal stripe.—In the terrestrial group there is little variation in the dorsal stripe, except in *vagrans*. Fitch (1940:17) described *vagrans* as having a dull, yellowish or brownish dorsal stripe which is much less pronounced than that of the other races of the group. This feature may be correlated with the partly aquatic habits of this race.

A very bright dorsal stripe is present in *elegans* and *hueyi*, and one almost equally bright is present in *terrestris*. In these races it is yellow or orange yellow. In all but *vagrans* it is usually $\frac{1}{2}$ -1- $\frac{1}{2}$ scale rows in width.

Variation in dorsolateral color.—Dorsolateral ground color is very stable in *elegans* and *hueyi*, and only moderately variable in *vagrans*. Although *elegans* is rather uniformly black throughout most of its range, it is dark brown in areas where it intergrades with *vagrans* and *biscutatus* (Fitch, 1940:37). *Hueyi* also exhibits somber tones—dark brown or dark olive. The dorsolateral region of *vagrans* is typically brown, pale brown, or tan, although that of the population from British Columbia which Johnson (1947) described as *T. e. nigrescens* is dark brown or black.

In *terrestris*, however, there is considerable variation. Reddish-brown dorsolateral ground color is characteristic of many snakes in areas bordering San Francisco Bay. Snakes of this color occur in small numbers as far north as Mendocino County and as far south as Monterey County. Olive brown and olive gray usually replace the reddish brown, north and south of the San Francisco Bay region. Specimens from the eastern part of the Bay area are reddish brown or olive brown. Those from the more eastern canyons of the Coast Ranges situated east of the bay are very dark, almost black. In this characteristic they bear a strong resemblance to *elegans*.

Bright red blotches are present in varying amounts on the sides, belly, and dorsolateral areas. Specimens from localities east of San Francisco Bay are most conspicuously marked, whereas those to the north and south tend to have less red. Specimens with appreciable amounts of red are not common in most areas of the northern part of the range of the subspecies, except around Crescent City; all specimens from that area are brightly marked with red on the sides and even in the dorsal stripe. Although *terrestris* is the only race of the species *Thamnophis elegans* that typically has these bright red pigments, such pigments are a prominent feature of the sympatric species *T. ordinoides*. This similarity in pigmentation is one of the chief supports for the postulation of a close relationship between *terrestris* and *ordinoides*.

Variation in scutellation.—The column on the left in figure 11 shows the north-south variation in numbers of gastrosteges in *T. e. terrestris*. The average numbers of these scutes in the sample from Del Norte County are significantly higher than in the sample from the coastal areas of Mendocino County. The coastal samples from Mendocino to Monterey counties show no significant variation in this character. The sample from Alameda and Contra Costa counties is composed of snakes from localities slightly more interior. This sample has larger numbers of gastrosteges and urosteges than the coastal samples have. Urosteges in specimens from the south are fewer than in those from the north, the decrease being gradual but significant (fig. 12).

From the northern to the southern part of the range, there is a gradual increase in the number of scale rows around the body of *terrestris* (table 1). The number of scale rows at the neck is a variable character and shows a weak trend toward an increase from 19 to 21. Scale rows at the thoracic region are predominately 19 at the northern end of the range and predominately 21 at the southern end of the range. Although characteristically there are 17 scale rows at the posterior end of the body throughout the entire range of the subspecies, the percentage of individuals with this number is higher in the southern populations.

Eight supralabials, 10 infralabials, 1 preocular, and 3 postoculars are characteristic of the species *T. elegans*. Variations from this characteristic condition occur but are of little diagnostic value. Table 2 shows that the tendency toward a reduction in the number of labials is significantly increased in the northern populations of *T. e. terrestris*. The occurrence of two preoculars is not rare in *terrestris*. Data presented in table 2 indicate a higher frequency of divided preoculars in samples from the central part of its range. However, this division of the preocular does not appear to be clearly correlated with either geography or environment. Postoculars show a higher degree of variation in the more northern populations.

Fitch (1940) carefully analyzed scutellation in *biscutatus*, *elegans*, *vagrans*, and *hueyi*. Figures 4 and 5 show a very significant increase in the number of gastrosteges and urosteges, from *terrestris* eastward through the intergrading populations to *elegans*. *T. e. elegans* is characterized by large numbers of these scutes throughout the Sierra Nevada. The numbers decrease significantly in the San Bernardino Mountains, a trend which renders them intermediate between typical *T. e. elegans* and *T. e. hueyi*. Both the San Bernardino Mountains *elegans* and *T. e. hueyi* represent isolated mountain populations. *T. e. hueyi* has greatly reduced numbers of gastrosteges and urosteges and in this respect bears a close resemblance to *T. e. terrestris*. *T. e. biscutatus*, the link between the terrestrial and aquatic groups, is intermediate between *hydrophila* and *elegans* in the number of these scutes. *T. e. vagrans* from northern Nevada and southeastern Oregon has a relatively large number of ventral scutes; the minimum numbers of scutes appear in the extreme northern and southern parts of its range (Fitch, 1940:19). *T. e. nigrescens* has significantly fewer scutes than has *vagrans* from eastern Washington, Idaho, or Nevada. It is similar to *vagrans* from New Mexico and Arizona (Fitch, 1948:123).

The interior races of the terrestrial group show little variation in the maximum number of scale rows. Typically, there are 21, although Fitch (1940:33) states that there is a tendency toward the shortening of the "6th" scale row in *elegans*.

Comparison of scutellation in the aquatic and terrestrial groups.—It seems pertinent at this point to indicate certain significant differences in the geographic variation of scutellation among the coastal populations of the two groups. Within the terrestrial group, the typical number of scale rows in the thoracic region tends to shift from 19 in the more northern populations to 21 in the more southern populations (table 1). Although in the more northern populations of the aquatic group, 19 and 21 scale rows appear with almost equal frequency, individuals with 21 scale rows are almost completely lacking in the more southern populations (table 1). This tendency for a decrease in the number of scale rows in more southern areas is a direct reversal of the trend which appears in the terrestrial group.

The geographic variation in numbers of gastrosteges and urosteges is more pronounced within the aquatic group. Although the number of gastrosteges in the aquatic races is significantly reduced from Del Norte to Monterey counties, the number of these scutes remains practically uniform in the coastal populations of the terrestrial group (fig. 11). Likewise, although in the number of urosteges the terrestrial group shows only a slight decline from north to south, the southern populations of the aquatic form show a significant reduction in the number of these scutes (fig. 12).

Certain irregularities of the head scutes are also more common in one or the other of the two main groups. The terrestrial races have a greater tendency for reduction in the number of supralabials and infralabials (table 2). The tendency for an increase of the infralabials from 10 to 11 is significantly greater in the aquatic races. Divided preoculars are characteristic of the race *biscutatus* and are consequently present in high frequencies in populations of *elegans* and *hydrophila* that are influenced by intergradation with it. *Hammondi* and *nigrescens* also have high frequencies of occurrence of divided preoculars. Aside from this, in most pop-

ulations of *terrestris*, divided preoculars occur with significantly greater frequency than in any other of the populations which have been analyzed (table 2). *Terrestris* likewise has a significantly greater disturbance of the typical postocular pattern than the coastal populations of the aquatic group have.

EVIDENCE OF SPECIATION

Fitch (1940, 1948) has discussed the evolutionary trends within *Thamnophis elegans* and related species, but certain aspects of the situation should be reemphasized. There is greater variation within this single species than within many genera of snakes. Within the genus *Thamnophis* no other species undergoes as diverse ecological and morphological differentiation as *elegans* does. Many of the racial characteristics are of the same nature as those which differentiate other races of snakes, but other racial characteristics are of the same nature as those which differentiate species.

In support of this interpretation it is worth while to review the intergradation that occurs between the aquatic and terrestrial groups.

Typical *T. e. hydrophila* occurs in the lower Klamath River, and up this drainage system it intergrades with *T. e. biscutatus* of the Klamath Lakes region, a form which is aquatic in habits but which morphologically is somewhat intermediate between the aquatic and terrestrial groups. Specimens found southeast of the Klamath Lakes region, in Modoc and Lassen counties, are intergrades between *biscutatus* and *elegans*. Morphologically, these snakes are typical of the terrestrial group, but they are of generalized habits. Farther south, east, and west of this area of intergradation are found *elegans* with typical terrestrial ecology and morphology. These inhabit certain areas in which there are *hydrophila* and *hydrophila-biscutatus* intergrades, without interbreeding (Fitch, 1940: 29). Within this small loop of intergrading populations (see fig. 13) occur sufficient differentiation to render incompatible the overlapping arms of the loop represented by the terrestrial and aquatic groups. These two groups are sympatric over most of California (figs. 6 and 7) and are distinct both morphologically and ecologically. Except for the fact that they are linked by intergrading populations through the loop described above, either the divergent morphology or ecology would be sufficient basis for designating them as distinct species.

Another example of range overlap without intergradation occurs within the aquatic group itself, where *T. e. atratus* overlaps the range of *T. e. hammondi* throughout the coastal parts of Monterey and San Luis Obispo counties (fig. 6). Although these two races are placed in the same ecological group, *atratus* has adopted semiterrestrial habits, as I have previously pointed out, and consequently the two forms are probably only slightly competitive. Morphologically they are distinct in many basic characters.

It is not known whether any two sympatric subspecies of the *elegans* rassenkreis attempt to interbreed in the wild. Due to the difficulty of breeding snakes in captivity, I have not been able to test for interfertility between members of the terrestrial and members of the aquatic group. However, since there are no known hybrids in regions where members of the two groups occur together, there is reason to believe that they behave toward each other as distinct species.

The ecological segregation is not sharp enough to prevent individual contact. Although the members of the aquatic group are quite distinct from those of the terrestrial group in feeding habits and in defense and escape reactions, they are not completely isolated from each other. In general, the aquatic form is found near water, whereas the terrestrial form is not dependent upon bodies of water. However, they live along the banks of streams and ponds in the same area, and it is not

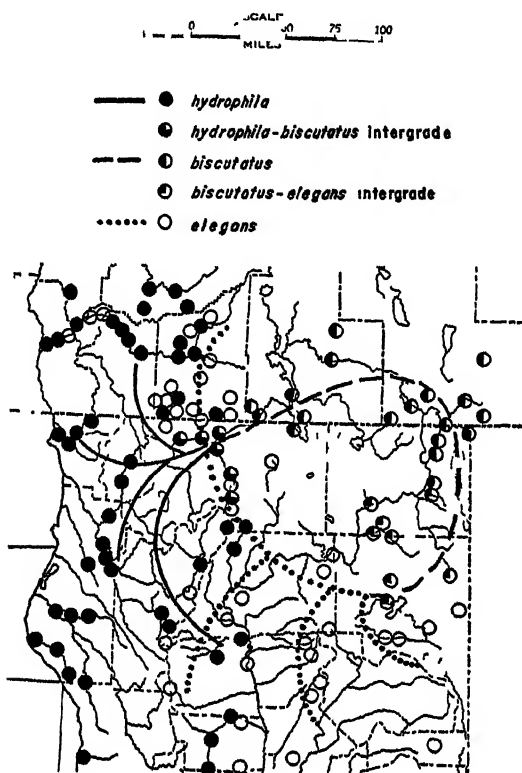


Fig. 13. Map of northern California and southern Oregon showing critical area of intergradation between aquatic and terrestrial groups. Circles represent locality records. Complex loop illustrates path of intergradation from *hydrophila* through *biscutatus* to *elegans* and overlapping of *hydrophila* and *elegans* without interbreeding.

uncommon to find several representatives of both groups taking shelter under the same piece of surface litter such as a board or a sheet of metal.

So far as is known, all the subspecies of the rassenkreis breed in the spring soon after emergence from hibernation. There are no morphological barriers which would prevent copulation between any of these subspecies. On several occasions I have found individuals of two sympatric subspecies, *T. e. atratus* and *T. e. terrestris*, together during the breeding season. Although there appears to be ample opportunity for interbreeding between the sympatric forms, there is no evidence that this takes place.

Elsewhere I have pointed out the sympatric relationship of *T. ordinoides* and *T. e. terrestris* and their strong morphological similarity (Fox, 1948). Many of the similarities and differences (e.g., distribution of red pigment, scutellation, and pattern) are of the kind routinely found in geographic races. Other variations (head shape, body proportions, and behavior) are characteristic of differences between species. It was postulated by both Fitch (1940) and Fox (1948) that *ordinoides* and *atratus* were once a continuously interbreeding population, that they became geographically isolated, and that upon renewal of contact they behaved as distinct species.

Chains of races in which the end forms overlap but do not interbreed have been described by various investigators (for review of literature see Goldschmidt, 1940; Mayr, 1942; Fitch, 1948). Recently, Stebbins (1949) has presented another interesting example of this phenomenon in the plethodontid salamander *Ensatina escholtzii*. In this polytypic species there are two parallel chains of races, one along the coast and one through the Sierra Nevada in California. There is primary intergradation between the northern ends of the chains, secondary intergradation at a central point of contact, and overlap without intergradation at the southern ends.

These examples of range overlap of subspecies without interbreeding suggest that some geographic races are approaching the species level. The strongest argument for speciation is the sympatric relationship of the terminal forms of the rassenkreis. The morphological differences are usually quantitative, and it is difficult to determine whether they are specific or subspecific in character. In the genus *Thamnophis* there are several species and many subspecies from which one may judge the taxonomic importance of morphological and ecological characters. Admittedly, on the basis of these characters it is justifiable to claim that the differences between certain races of *T. elegans* are on the species level. However, breaking this chain of races into separate species would run counter to most modern species concepts (Mayr, 1942:113-120) since they are geographically complementary populations joined by primary intergradation. Consequently, I believe that these races should be regarded as a single species. Nevertheless, if morphology and ecology are reliable criteria for drawing conclusions about species formation, the two ecological groups of the *Thamnophis elegans* rassenkreis seem to represent two species in which the "bridgeless gap" is spanned by smoothly intergrading populations.

SUMMARY

1. Two forms of the *Thamnophis elegans* rassenkreis which occur in the vicinity of San Francisco Bay and which formerly have been regarded as color phases of the same subspecies, *T. e. atratus*, are recognized as morphologically and ecologically distinct subspecies which do not interbreed. One of these, *T. e. atratus*, is aquatic in habits and is linked to the aquatic *T. e. hydrophila* by mutual intergradation with another newly described aquatic subspecies, *T. e. aquaticus*, which occurs north of San Francisco Bay. *T. e. terrestris*, which is sympatric to the above-mentioned aquatic races, is terrestrial in habits and interbreeds with the terrestrial race *T. e. elegans*.

2. The *Thamnophis elegans* rassenkreis can be divided into two ecological units, one aquatic and the other terrestrial. The races within each of these groups are

allopatric (with one exception in the aquatic group), whereas the groups themselves are largely sympatric to each other. Fitch's claim (1940) that the rassenkreis is composed of smoothly intergrading populations has been verified in the present study.

3. Many steps of the process of speciation can be seen in Pacific coast garter snakes. A few races of *T. elegans* are distinguished on the basis of slight differences in color, pattern, or scale characters and scarcely appear to be incipient species. Another garter snake, *T. ordinoides*, although closely related morphologically to the *elegans* rassenkreis, has apparently reached the full species status. Between these two extremes lie the rest of the races of the *elegans* rassenkreis. The marked ecological and morphological differences, as well as the overlapping without interbreeding of several of these subspecies, suggest that species formation is in progress and has nearly been accomplished. However, since the chain of races is at the present time a continuous series of interbreeding populations, it is my opinion that they should all be included in the same species.

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AN ANALYSIS OF THE DISTRIBUTION OF THE BIRDS OF CALIFORNIA

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AN ANALYSIS OF THE DISTRIBUTION OF THE BIRDS OF CALIFORNIA

BY

ALDEN H. MILLER

(Contribution from the Museum of Vertebrate Zoology of the University of California)

INTRODUCTION

THE BIRDS of California have received intensive scrutiny to a degree that warrants renewed effort to draw some generalizations from the wealth of data concerning their differentiation and distribution. Such an effort was envisioned when the basic facts were compiled in a book on the distribution of the birds of California in 1944 (Grinnell and Miller). Some impatience has arisen from the fact that analyses and generalizations were not attempted in conjunction with this preceding factual summation. Actually, that account of affairs, species by species, with its data on the habitat and distributional limits of each, may be a more substantial scientific record than the generalized review here set forth.

Efforts to develop broad distributional principles and categories commonly run beyond the facts and violate the essentially statistical character of distributional data. There is an urge to create simplified concepts, perhaps unwittingly as paths of least intellectual resistance. These may become lines of escape from exhaustive factual comprehension. Realization of such dangers is helpful to author and reader alike in approaching a treatise of generalized character.

We may acknowledge, to begin with, that we are unable to resolve distributional patterns into a neat system comparable to the periodic table of chemistry, the chromosome map of genetics, or even the imperfect phyletic taxonomy of the systematist. There is no single sequential organization of distributional data. We are confronted with the end results of an array of delicate and complicated equilibria, in which the spatial balance of each species is a phenomenon peculiar to itself because of heritable differences interacting with the influences of many other species and of inorganic factors.

There have been three general plans for grouping distributional information which have been applied extensively to terrestrial animals in North America. These are the zone, biome, and biotic province systems. Each has had modifications and associated auxiliary systems. For example, the system of differentiation centers is related to, but is by no means identical with, the province system. The province system has been particularly vague because no adequate definition of a biotic province has been offered and the units in it are usually subjectively determined (see critique by Johnson, Bryant, and Miller, 1948). The three major plans have indeed some common basis, namely climatic and consequent vegetational factors, but each has its special emphasis and some criteria for its divisions which are peculiar to it. Accordingly, we may not regard any one system as a master system to which others are subordinate, as Grinnell at one time (1915) and Aldrich (Aldrich and Friedmann, 1943:89) have undertaken in different ways to show. Rather, each system has some, although perhaps not equal, usefulness and expresses certain truths. I shall attempt, therefore, to assort the data for native birds, as one group of vertebrates, in accordance with my concepts of the major distributional

systems, modifying them as seems required, pointing out some generalities which each reveals, and coördinating the several plans to the degree that seems permissible.

The names employed in this paper, both vernacular and scientific, are those advocated by Grinnell and Miller (1944), with a few supplementary changes and additions summarized on pages 619-621 of this paper.

LIFE-ZONES

The life-zone system is based on the concept of occurrence of similar organic life throughout belts where the same temperature phenomena prevail. Just what these temperature phenomena are has been the source of considerable confusion and debate which need not be reviewed here (see Kendeigh, 1932; Shelford, 1932; Grinnell, 1935; Daubenmire, 1938). Although the exact components of "gross temperature" characteristic of each zone have not been determined satisfactorily, one cannot escape the fact that recognizable zones or belts of life exist which follow one another latitudinally or altitudinally in a sequence according with temperature gradients. Where the gradients are steep, as in altitudinally diverse terrain, the belts are more obvious, long transitions between zones are eliminated, and influences other than temperature are overshadowed. Anyone can "see" life-zones or temperature-correlated plant belts on mountain slopes. This circumstance was the stimulus and sound foundation of the system. Its weakness lies in the extension of a set of zones developed on one mountain slope into a continent-wide plan. The fact is that under different conditions of rainfall and humidity, with diverse quantitative and seasonal aspects, sets of organisms occur in the same temperature belt which are so different that there is only a weak common faunal element throughout, a situation admitted only in part by Merriam, the founder of the system. In practice, one well-known set of life-zones must be observed in its gradation into another set in an adjoining area to establish correspondence of units; assumptions are then made that there is a comparable temperature environment in the two. In this way a correlated zonal stratification may be recognized over a wide area.

Because of these considerations, zones may be expected to show some reality and constancy in an area the size of California, which has conspicuous mountain ranges. But even here, comparable levels with similar summer temperatures show marked differences because of humidity, rainfall, and edaphic factors, as one progresses inward from the coast, and particularly on crossing the Sierran and desert divides. For example, the Transition Zone of western California is not easily identified with the Transition Zone of the Great Basin. For a mapping of zones and for zonal indicators (in effect, plant associations) which serve to identify and set boundaries for them, see Grinnell (1935) and Hall and Grinnell (1919).

There are six life-zones in California, of which the coolest, the Alpine-Arctic, is but poorly developed. The five important zones provide a smaller array of categories than do the other distributional systems later to be considered. Thus each division is broader and cruder than those of the other plans. Birds are classed as to zone only in respect to breeding residence and only those of nonmarine breeding environment are treated. Each species is recorded as a unit, to include all its sub-

species. There are, to be sure, instances of subspecies of the same species with different zonal distribution, and this may in a few instances represent actual differences in zonal tolerance, as appears to be true in the races of white-crowned sparrow (*Zonotrichia leucophrys*). However, subspecies with different zonal range are often restricted geographically in a way that prevents them from revealing their full span of zonal tolerance. For general purposes, then, zonal range is best recorded by species units.

In tabulating zonal occurrence, certain casual occurrences beyond normal zonal limits have been disregarded, and limited spatial transgression of zonal boundaries, even by numbers of individuals, has been ruled out. These decisions have necessarily been arbitrary, as no precise standards can be set for exclusion of data. The endeavor has been to indicate the main truth of zonal occurrence, not the occasional exceptions. Even within the normal zonal range it is evident to a field observer that there is greater concentration of a species in one zone, or one part of a zone, than in another. An effort to register this situation was made by Grinnell and Storer (1924) in their diagrams of zonal occurrence in the Yosemite area. But since extensive data on population density are lacking, this is not attempted now for the state as a whole. Compiled observations of habitat preference of a qualitative kind have led me to attempt a preference rating for ecologic formations in a succeeding section. Further, it should be realized that any one species may not occur throughout the geographic area of the zone or zones to which it is restricted or, indeed, in all the ecologic facies of that zone at any one place. The same conditions pertain to occurrences in relation to major ecologic categories.

The total number of species tabulated is 260. Totals by zone (table 1) show the greatest numbers in the Upper Sonoran and the Transition zones, with 67 and 68 per cent of the grand total. There follow, with progressively smaller lists of species, the Lower Sonoran (55), the Canadian (33), and the Hudsonian (13). The representation in the Alpine-Arctic is quantitatively negligible. An important fact derived from table 2 is that most species have a zonal range of two or three units. Fewer are confined to a single zone, yet very few occur in four or more zones.

The idea has been expressed many times that the zones are of unequal value, the distinction between certain adjacent zones being greater than that between others. The degree to which this may be true is partly indicated by the avifauna. If lists of adjoining zones are compared, we may record the total number of species that occurs in one but not in the other. This reflects both differences in make-up of zonal faunas of similar size and contrast in faunas owing to differential size. Both are reflections of zonal difference. This type of comparison shows the greatest differential between Upper Sonoran and Transition (103) and Transition and Canadian (102). The contrasts between Upper Sonoran and Lower Sonoran (82), Canadian and Hudsonian (50), and Hudsonian and Alpine-Arctic (84) are much less.

Another method of comparison is to summate the species in common to adjoining zones and express this as percentage of the smallest of the two zonal faunas (see Simpson, 1947). This shows resemblance of the faunas apart from differential size. The comparison of Alpine-Arctic is not sensible because of its extremely small avifauna. The greatest resemblance of adjoining zones is that of Canadian and Hudsonian (100 per cent) which means that the entire contrast of the two is the

TABLE 1
OCCURRENCE OF BREEDING BIRDS IN LIFE-ZONES IN CALIFORNIA

	Lower Sonoran	Upper Sonoran	Transition	Canadian	Hudsonian	Alpine-Arctic
<i>Gavia immer</i> , Common Loon.....			x	x		
<i>Colymbus caspicus</i> , Eared Grebe.....	x	x	x			
<i>Colymbus dominicus</i> , Least Grebe.....	x					
<i>Aechmophorus occidentalis</i> , Western Grebe.....	x	x	x			
<i>Podilymbus podiceps</i> , Pied-billed Grebe.....	x	x	x			
<i>Pelecanus erythrorhynchos</i> , White Pelican.....	x	x	x			
<i>Phalacrocorax auritus</i> , Double-crested Cormorant.....	x	x	x			
<i>Ardea herodias</i> , Great Blue Heron.....	x	x	x			
<i>Butorides virescens</i> , Green Heron.....	x	x				
<i>Casmerodius albus</i> , Common Egret.....	x	x				
<i>Leucophoyx thula</i> , Snowy Egret.....	x	x				
<i>Nycticorax nycticorax</i> , Black-crowned Night Heron.....	x	x	x			
<i>Izobrychus exilis</i> , Least Bittern.....	x	x				
<i>Botaurus lentiginosus</i> , American Bittern.....	x	x	x	x		
<i>Plegadis mexicana</i> , White-faced Glossy Ibis.....	x	x				
<i>Branta canadensis</i> , Canada Goose.....			x	x		
<i>Dendrocygna bicolor</i> , Fulvous Tree-duck.....	x	x				
<i>Anas platyrhynchos</i> , Mallard.....	x	x	x	x		
<i>Anas cyanoptera</i> , Cinnamon Teal.....	x	x	x			
<i>Anas discors</i> , Blue-winged Teal.....	x	x	x			
<i>Anas carolinensis</i> , Green-winged Teal.....		x	x			
<i>Anas acuta</i> , Pintail.....	x	x	x			
<i>Anas strepera</i> , Gadwall.....	x	x				
<i>Mareca americana</i> , Baldpate.....		x	x			
<i>Spatula clypeata</i> , Shoveller.....	x	x				
<i>Aix sponsa</i> , Wood Duck.....	x	x	x			
<i>Aythya valisineria</i> , Canvas-back Duck.....		x	x			
<i>Aythya americana</i> , Redhead Duck.....	x	x				
<i>Bucephala islandica</i> , Barrow Golden-eye.....				x	x	
<i>Bucephala albeola</i> , Buffle-head Duck.....			x			
<i>Histrionicus histrionicus</i> , Harlequin Duck.....			x	x	x	
<i>Oxyura jamaicensis</i> , Ruddy Duck.....	x	x	x			
<i>Mergus merganser</i> , Common Merganser.....			x	x		
<i>Cathartes aura</i> , Turkey Vulture.....	x	x	x	x		
<i>Gymnogyps californianus</i> , California Condor.....		x	x			
<i>Elanus leucurus</i> , White-tailed Kite.....		x				
<i>Accipiter gentilis</i> , Goshawk.....				x		
<i>Accipiter cooperii</i> , Cooper Hawk.....	x	x	x			
<i>Accipiter striatus</i> , Sharp-shinned Hawk.....			x			
<i>Buteo jamaicensis</i> , Red-tailed Hawk.....	x	x	x	x		
<i>Buteo lineatus</i> , Red-shouldered Hawk.....	x	x				
<i>Buteo swainsoni</i> , Swainson Hawk.....		x				
<i>Parabuteo unicinctus</i> , Harris Hawk.....	x					
<i>Aquila chrysaetos</i> , Golden Eagle.....	x	x	x	x	x	
<i>Haliaeetus leucocephalus</i> , Bald Eagle.....		x	x			
<i>Circus cyaneus</i> , Marsh Hawk.....	x	x	x	x		

TABLE 1—Continued

	Lower Sonoran	Upper Sonoran	Transi- tion	Can- adian	Hud- sonian	Alpine- Arctic
<i>Pandion haliaetus</i> , Osprey.....	x	x	x			
<i>Falco mexicanus</i> , Prairie Falcon.....	x	x				
<i>Falco peregrinus</i> , Duck Hawk.....		x	x			
<i>Falco sparverius</i> , Sparrow Hawk.....	x	x	x	x	x	
<i>Dendragapus fuliginosus</i> , Sooty Grouse.....			x	x	x	
<i>Bonasa umbellus</i> , Ruffed Grouse.....			x			
<i>Pedioecetes phasianellus</i> , Sharp-tailed Grouse...		x	x			
<i>Centrocercus urophasianus</i> , Sage Grouse.....		x	x			
<i>Oreortyx picta</i> , Mountain Quail.....		x	x	x		
<i>Lophortyx californica</i> , California Quail.....	x	x	x			
<i>Lophortyx gambelii</i> , Gambel Quail.....	x					
<i>Grus canadensis</i> , Sandhill Crane.....		x	x			
<i>Rallus longirostris</i> , Clapper Rail.....		x				
<i>Rallus limicola</i> , Virginia Rail.....	x	x	x	x		
<i>Porzana carolina</i> , Sora Rail.....	x	x	x			
<i>Laterallus jamaicensis</i> , Black Rail.....		x				
<i>Coturnicops noveboracensis</i> , Yellow Rail.....			x			
<i>Gallinula chloropus</i> , Black Gallinule.....	x	x				
<i>Fulica americana</i> , American Coot.....	x	x	x			
<i>Charadrius nivosus</i> , Snowy Plover.....	x	x	x			
<i>Charadrius vociferus</i> , Killdeer.....	x	x	x	x		
<i>Numenius americanus</i> , Long-billed Curlew.....		x	x			
<i>Actitis macularia</i> , Spotted Sandpiper.....			x	x		
<i>Catoptrophorus semipalmatus</i> , Willet.....		x	x			
<i>Capella delicata</i> , Wilson Snipe.....		x	x			
<i>Himantopus mexicanus</i> , Black-necked Stilt....	x	x				
<i>Recurvirostra americana</i> , American Avocet....	x	x				
<i>Steganopus tricolor</i> , Wilson Phalarope.....	x	x				
<i>Larus delawarensis</i> , Ring-billed Gull.....		x				
<i>Larus californicus</i> , California Gull.....		x	x			
<i>Larus atricilla</i> , Laughing Gull.....	x					
<i>Chlidonias niger</i> , Black Tern.....	x	x	x			
<i>Gelochelidon nilotica</i> , Gull-billed Tern.....	x					
<i>Hydroprogne caspia</i> , Caspian Tern.....	x	x				
<i>Sterna forsteri</i> , Forster Tern.....	x	x	x			
<i>Columba fasciata</i> , Band-tailed Pigeon.....		x	x			
<i>Zenaidura macroura</i> , Mourning Dove.....	x	x	x			
<i>Zenaida asiatica</i> , White-winged Dove.....	x					
<i>Columbigallina passerina</i> , Ground Dove.....	x					
<i>Coccyzus americanus</i> , Yellow-billed Cuckoo....		x				
<i>Geococcyx californianus</i> , California Road-runner	x	x				
<i>Tyto alba</i> , Barn Owl.....	x	x	x			
<i>Otus flammeolus</i> , Flammulated Owl.....			x	x		
<i>Otus asio</i> , Screech Owl.....	x	x	x			
<i>Bubo virginianus</i> , Horned Owl.....	x	x	x	x		
<i>Glaucidium gnoma</i> , Pigmy Owl.....		x	x			
<i>Micrathene whitneyi</i> , Elf Owl.....	x					
<i>Speotyto cunicularia</i> , Burrowing Owl.....	x	x	x			
<i>Strix occidentalis</i> , Spotted Owl.....		x	x			

TABLE 1—Continued

	Lower Sonoran	Upper Sonoran	Transi- tion	Can- adian	Hud- sonian	Alpino- Arctic
<i>Strix nebulosa</i> , Great Gray Owl.....				x		
<i>Asio wilsonianus</i> , Long-eared Owl.....	x	x	x			
<i>Asio flammeus</i> , Short-eared Owl.....	x	x	x	x		
<i>Aegolius acadicus</i> , Saw-whet Owl.....			x	x		
<i>Chordeiles acutipennis</i> , Trilling Nighthawk....	x					
<i>Chordeiles minor</i> , Booming Nighthawk.....			x	x	x	
<i>Phalaenoptilus nuttallii</i> , Poor-will.....	x	x	x			
<i>Chaetura vauxi</i> , Vaux Swift.....			x			
<i>Nephoecetes niger</i> , Black Swift.....			x			
<i>Aëronautus saxatalis</i> , White-throated Swift....	x	x	x			
<i>Archilochus alexandri</i> , Black-chinned Hummingbird.....	x					
<i>Calypte costae</i> , Costa Hummingbird.....	x	x				
<i>Calypte anna</i> , Anna Hummingbird.....		x				
<i>Selasphorus platycercus</i> , Broad-tailed Hummingbird.....		x	x			
<i>Selasphorus sasin</i> , Allen Hummingbird.....		x	x			
<i>Stellula calliope</i> , Calliope Hummingbird.....			x	x		
<i>Megaceryle alcyon</i> , Belted Kingfisher.....	x	x	x			
<i>Colaptes cafer</i> , Red-shafted Flicker.....	x	x	x	x		
<i>Colaptes chrysoides</i> , Gilded Flicker.....	x					
<i>Dryocopus pileatus</i> , Pileated Woodpecker.....			x	x		
<i>Centurus uropygialis</i> , Gila Woodpecker.....	x					
<i>Balanosphyra formicivora</i> , Acorn Woodpecker...		x	x			
<i>Asyndesmus lewis</i> , Lewis Woodpecker.....		x	x	x		
<i>Sphyrapicus varius</i> , Yellow-bellied Sapsucker...			x	x		
<i>Sphyrapicus thyroideus</i> , Williamson Sapsucker..			x	x	x	
<i>Dendrocopos villosus</i> , Hairy Woodpecker.....		x	x	x	x	
<i>Dendrocopos pubescens</i> , Downy Woodpecker....	x	x	x			
<i>Dendrocopos scalaris</i> , Ladder-backed Wood- pecker.....	x					
<i>Dendrocopos nuttallii</i> , Nuttall Woodpecker....	x	x				
<i>Dendrocopos albolarvatus</i> , White-headed Woodpecker.....			x	x		
<i>Picoides arcticus</i> , Arctic Three-toed Wood- pecker.....				x	x	
<i>Tyrannus tyrannus</i> , Eastern Kingbird.....		x				
<i>Tyrannus verticalis</i> , Western Kingbird.....	x	x				
<i>Tyrannus vociferans</i> , Cassin Kingbird.....	x	x				
<i>Myiarchus cinerascens</i> , Ash-throated Flycatcher	x	x				
<i>Sayornis nigricans</i> , Black Phoebe.....	x	x	x			
<i>Sayornis saya</i> , Say Phoebe.....	x	x				
<i>Empidonax traillii</i> , Traill Flycatcher.....	x	x	x	x		
<i>Empidonax hammondi</i> , Hammond Flycatcher..				x		
<i>Empidonax wrightii</i> , Wright Flycatcher.....			x	x	x	
<i>Empidonax griseus</i> , Gray Flycatcher.....		x				
<i>Empidonax difficilis</i> , Western Flycatcher.....		x	x			
<i>Contopus richardsonii</i> , Western Wood Pewee...		x	x	x	x	
<i>Nuttallornis borealis</i> , Olive-sided Flycatcher...			x	x		

TABLE 1—Continued

	Lower Sonoran	Upper Sonoran	Transi- tion	Can- adian	Hud- sonian	Alpine- Arctic
<i>Pyrocephalus rubinus</i> , Vermilion Flycatcher....	x					
<i>Eremophila alpestris</i> , Horned Lark.....	x	x		x	x	x
<i>Thachycineta thalassina</i> , Violet-green Swallow..		x	x			
<i>Iridoprocne bicolor</i> , Tree Swallow.....	x	x	x	x		
<i>Riparia riparia</i> , Bank Swallow.....	x	x				
<i>Stelgidopteryx ruficollis</i> , Rough-winged Swallow	x	x	x			
<i>Hirundo rustica</i> , Barn Swallow.....	x	x	x			
<i>Petrochelidon pyrronota</i> , Cliff Swallow.....	x	x	x	x		
<i>Progne subis</i> , Purple Martin.....	x	x	x			
<i>Perisoreus canadensis</i> , Canada Jay.....			x	x		
<i>Cyanocitta stelleri</i> , Steller Jay.....		x	x	x		
<i>Aphelocoma coerulescens</i> , Scrub Jay.....	x	x	x			
<i>Pica pica</i> , Black-billed Magpie.....		x	x			
<i>Pica nuttallii</i> , Yellow-billed Magpie.....	x	x				
<i>Corvus corax</i> , Holarctic Raven.....	x	x	x	x		
<i>Corvus brachyrhynchos</i> , American Crow.....	x	x	x			
<i>Gymnorhinus cyanocephalus</i> , Piñon Jay.....		x				
<i>Nucifraga columbiana</i> , Clark Nutcracker.....			x	x	x	
<i>Parus atricapillus</i> , Black-capped Chickadee....			x			
<i>Parus gambeli</i> , Mountain Chickadee.....			x	x	x	
<i>Parus rufescens</i> , Choptnut-backed Chickadee...			x	x		
<i>Parus inornatus</i> , Plain Titmouse.....		x				
<i>Auriparus flaviceps</i> , Verdin.....	x					
<i>Psaltiriparus minimus</i> , Bush-tit.....	x	x	x			
<i>Sitta carolinensis</i> , White-breasted Nuthatch....		x	x	x	x	
<i>Sitta canadensis</i> , Red-breasted Nuthatch.....			x	x	x	
<i>Sitta pygmaea</i> , Pigmy Nuthatch.....			x			
<i>Certhia familiaris</i> , Brown Creeper.....			x	x		
<i>Chamaea fasciata</i> , Wren-tit.....		x	x			
<i>Cinclus mexicanus</i> , American Dipper.....			x	x	x	
<i>Troglodytes aëdon</i> , House Wren.....		x	x	x		
<i>Troglodytes troglodytes</i> , Winter Wren.....			x	x		
<i>Thryomanes bewickii</i> , Bowick Wren.....	x	x	x			
<i>Campylorhynchus brunneicapillus</i> , Cactus Wren.	x					
<i>Telmatorhynchus palustris</i> , Marsh Wren.....		x	x			
<i>Catherpes mexicanus</i> , Canyon Wren.....	x	x	x			
<i>Salpinctes obsoletus</i> , Rock Wren.....	x	x	x	x	x	
<i>Mimus polyglottos</i> , Mockingbird.....	x	x				
<i>Oreoscoptes montanus</i> , Sage Thrasher.....		x	x	x	x	
<i>Toxostoma bendirei</i> , Bendire Thrasher.....	x					
<i>Toxostoma lecontei</i> , LeConte Thrasher.....	x					
<i>Toxostoma redivivum</i> , California Thrasher.....	x	x				
<i>Toxostoma dorsale</i> , Crissal Thrasher.....	x					
<i>Turdus migratorius</i> , Robin.....		x	x	x	x	
<i>Ixoreus naevius</i> , Varied Thrush.....			x			
<i>Hylocichla guttata</i> , Hermit Thrush.....			x	x	x	
<i>Hylocichla ustulata</i> , Swainson Thrush.....		x	x	x		
<i>Sialia mexicana</i> , Mexican Bluebird.....	x	x	x	x		
<i>Sialia currucoides</i> , Mountain Bluebird.....			x	x	x	

TABLE 1—Continued

	Lower Sonoran	Upper Sonoran	Transi- tion	Can- adian	Hud- sonian	Alpine- Arctic
<i>Myadestes townsendi</i> , Townsend Solitaire.....			x	x	x	
<i>Poliophtila caerulea</i> , Blue-gray Gnatcatcher.....	x	x				
<i>Poliophtila melanura</i> , Black-tailed Gnatcatcher..	x					
<i>Regulus satrapa</i> , Golden-crowned Kinglet.....			x	x		
<i>Regulus calendula</i> , Ruby-crowned Kinglet.....			x	x	x	
<i>Bombycilla cedrorum</i> , Cedar Waxwing.....			x			
<i>Phainopepla nitens</i> , Phainopepla.....	x	x				
<i>Lanius ludovicianus</i> , Loggerhead Shrike.....	x	x				
<i>Vireo huttoni</i> , Hutton Vireo.....		x	x			
<i>Vireo bellii</i> , Bell Vireo.....	x					
<i>Vireo vicinior</i> , Gray Vireo.....		x				
<i>Vireo solitarius</i> , Solitary Vireo.....			x	x		
<i>Vireo gilvus</i> , Warbling Vireo.....		x	x	x		
<i>Vermivora celata</i> , Orange-crowned Warbler....		x	x	x		
<i>Vermivora ruficapilla</i> , Nashville Warbler.....			x	x		
<i>Vermivora virginiae</i> , Virginia Warbler.....			x			
<i>Vermivora luciae</i> , Lucy Warbler.....	x					
<i>Dendroica aestiva</i> , Yellow Warbler.....	x	x	x			
<i>Dendroica auduboni</i> , Audubon Warbler.....			x	x	x	
<i>Dendroica nigrescens</i> , Black-throated Gray Warbler.....		x	x			
<i>Dendroica occidentalis</i> , Hermit Warbler.....			x	x		
<i>Oporornis tolmiei</i> , Tolmie Warbler.....			x	x		
<i>Geothlypis trichas</i> , Yellow-throat.....	x	x	x			
<i>Icteria virens</i> , Chat.....	x	x	x			
<i>Wilsonia pusilla</i> , Pileolated Warbler.....		x	x	x		
<i>Dolichonyx oryzivorus</i> , Bobolink.....		x				
<i>Sturnella neglecta</i> , Western Meadowlark.....	x	x	x			
<i>Xanthocephalus xanthocephalus</i> , Yellow-headed Blackbird.....	x	x	x			
<i>Agelaius phoeniceus</i> , Red-winged Blackbird....	x	x	x			
<i>Agelaius tricolor</i> , Tricolored Blackbird.....	x	x				
<i>Icterus cucullatus</i> , Hooded Oriole.....	x	x				
<i>Icterus parisorum</i> , Scott Oriole.....	x	x				
<i>Icterus bullockii</i> , Bullock Oriole.....	x	x	x			
<i>Euphagus cyanocephalus</i> , Brewer Blackbird....	x	x	x	x		
<i>Molothrus ater</i> , Brown-headed Cowbird.....	x	x	x			
<i>Piranga ludoviciana</i> , Western Tanager.....			x	x	x	
<i>Piranga rubra</i> , Summer Tanager.....	x					
<i>Richmondia cardinalis</i> , Cardinal.....	x					
<i>Pheucticus melanocephalus</i> , Black-headed Grosbeak.....	x	x	x			
<i>Guiraca caerulea</i> , Blue Grosbeak.....	x					
<i>Passerina amoena</i> , Lazuli Bunting.....	x	x	x			
<i>Hesperiphona vespertina</i> , Evening Grosbeak....			x	x		
<i>Carpodacus purpureus</i> , Purple Finch.....		x	x			
<i>Carpodacus cassinii</i> , Cassin Finch.....			x	x	x	
<i>Carpodacus mexicanus</i> , House Finch.....	x	x	x			
<i>Pinicola enucleator</i> , Pine Grosbeak.....				x	x	

TABLE 1—*Concluded*

	Lower Sonoran	Upper Sonoran	Transi- tion	Can- adian	Hud- sonian	Alpine- Arctic
<i>Leucosticte tephrocotis</i> , Rosy Finch.....						x
<i>Spinus pinus</i> , Pine Siskin.....			x	x	x	
<i>Spinus tristis</i> , American Goldfinch.....	x	x	x			
<i>Spinus psaltria</i> , Arkansas Goldfinch.....	x	x	x			
<i>Spinus lawrencei</i> , Lawrence Goldfinch.....	x	x	x			
<i>Loxia curvirostra</i> , Red Crossbill.....			x	x	x	
<i>Chlorura chlorura</i> , Green-tailed Towhee.....			x	x		
<i>Pipilo maculatus</i> , Spotted Towhee.....	x	x	x			
<i>Pipilo fuscus</i> , Brown Towhee.....	x	x	x			
<i>Pipilo aberti</i> , Abert Towhee.....	x					
<i>Passerculus sandwichensis</i> , Savannah Sparrow..	x	x	x			
<i>Ammodramus savannarum</i> , Grasshopper Sparrow	x	x	x			
<i>Poocetes gramineus</i> , Vesper Sparrow.....		x	x	x		
<i>Chondestes grammacus</i> , Lark Sparrow.....	x	x	x			
<i>Aimophila ruficeps</i> , Rufous-crowned Sparrow...		x				
<i>Amphispiza bilineata</i> , Black-throated Sparrow..	x	x				
<i>Amphispiza belli</i> , Bell Sparrow.....	x	x				
<i>Junco oreganus</i> , Oregon Junco.....		x	x	x	x	
<i>Junco caniceps</i> , Gray-headed Junco.....			x			
<i>Spizella passerina</i> , Chipping Sparrow.....	x	x	x	x	x	
<i>Spizella breweri</i> , Brewer Sparrow.....		x	x	x	x	
<i>Spizella atrogularis</i> , Black-chinned Sparrow....		x				
<i>Zonotrichia leucophrys</i> , White-crowned Sparrow.		x	x	x	x	x
<i>Passerella iliaca</i> , Fox Sparrow.....			x	x		
<i>Melospiza lincolni</i> , Lincoln Sparrow.....			x	x	x	
<i>Melospiza melodia</i> , Song Sparrow.....	x	x	x			
Totals.....	143	174	177	86	35	3

TABLE 2
TOTAL ZONAL RANGE OF BREEDING BIRDS

Zonal range	Number of species	Percentage
1.....	54	21
2.....	89	34
3.....	88	34
4.....	23	9
5.....	5	2
6.....	1	..
	260	

result of difference in size—the absence of Canadian species in the Hudsonian. The next highest resemblance is that of Transition and Canadian at 93 per cent; the strong difference of the two shown by the index of difference is due mainly to differential size—the relative impoverishment of the Canadian fauna. The resemblance index for Lower Sonoran and Upper Sonoran is 82 per cent, and the lowest resemblance is that of Upper Sonoran and Transition at 71.

Considering both methods of quantitative expression of relationship, we may conclude that for the avifauna of California the contrast of Upper Sonoran and Transition is the greatest. The contrast of Upper Sonoran and Lower Sonoran and of Transition and Canadian are roughly equivalent, the former with somewhat more emphasis on qualitative difference, the latter on size difference. The distinction of Canadian and Hudsonian is much less important, being solely a depletion of the fauna in the higher zone. The same may be said of the contrast of Alpine-Arctic and Hudsonian; an exception here is the occurrence of *Leucosticte tephrocotis*, which is strictly an Alpine-Arctic type of bird.

For purposes of showing zonal relations and importance in California we may justifiably group the three cool zones (Canadian, Hudsonian, and Alpine-Arctic) as subzones of an inclusive Boreal Zone, as has frequently been done, but heretofore without well-defined basis. Four major life-zones would then be recognized: Lower Sonoran, Upper Sonoran, Transition, and Boreal, with a major division, for California at least, between Upper Sonoran and Transition. It is well to caution that in other areas and with other segments of the biota this rating of zones and their degrees of contrast may not fit the facts.

ECOLOGIC FORMATIONS

The selection of a set of ecologic formations in terms of which the distribution of birds may be described and classified has presented the question of the degree to which subdivision would be useful. Merely the broadest categories of plant formations or biomes, such as forest, grassland, woodland, and scrub, seem too gross, especially when the distinctive categories of chaparral, sagebrush, and desert scrub would in such a classification fall in a single unit. Greater meaning is derived from employing units of lesser rank, more or less equivalent to the second- and third-order subdivisions in Weaver and Clements' listing (1938). Even these obviously are subdivisible, but it is thought that the total number of units must be held down to serve the general purpose and that the listing must not descend to the level of particular plant associations. Hence the piñon-juniper formation includes the Joshua tree association, which is obviously very different from piñon woodland yet has similarities in life-form and reflects a related type of climate.

The selection of units is not made necessarily in reference to the successional history of plants. The birds concerned are certainly not aware of these histories, and even the plant ecologist does not know them well for many situations in the West. The occurrence of a particular aggregation of plants and animals at a particular time is the reflection of complex equilibria, and I doubt that change in these equilibria should be viewed as invariably being along one line of succession; times of sequence may at times be diverted, if not reversed, or may be blocked indefinitely. Emphasis in selecting units has been placed on life-form (Pitelka, 1941) the plant cover, or on the physical aspects of rock and aquatic habitats, these

being of utmost importance in the uses which different species of birds can make of them in exercising their instincts for foraging, nesting, and seeking shelter. Birds and other highly mobile animals usually adjust their distribution quickly to the current environmental situation. They preserve few local features of distribution which contribute to knowledge of successional history; they adjust to the successional change with little or no lag.

Each formation is not to be viewed as of equal value. Some are more uniform; others are distinct mixtures or are clearly divisible into subcategories. In the accounts of formations which follow, the critical features of life-form and physical setting of each are briefly indicated, and usually also, for the terrestrial units, some of the dominant plants present. In general terms the zonal and geographic distribution of each in the state is given.

There are 274 species of birds that breed in California about which sufficient is known of their summer habitat to justify classification ecologically. Under each formation the species occurring therein are listed with a superior number showing whether the affinity to the formation is of first importance or of secondary or lesser importance; thus some species are listed for five to ten formations, one even for thirteen of the twenty-one possible formations. Ratings are based on the greatest concentrations of the species and on the provision of the most critical and limiting factor from the standpoint of existence of the bird concerned. The formation rated as "2" for a species may be almost as important as formation 1 or of much less significance; it may represent a normally combined use of 1 and 2 in which 2 seems a somewhat less vital or a more easily replaced element in the combination; probably in some such circumstances the second element is really of equal importance. Obviously, when many formations, six or more, are involved, the exact seriation has little meaning, and indeed the classification of the species in the system may be futile. However, for completeness all such eurytopic species are listed and serve at least to show the size of the group of birds whose affinities to formations are many and not particularly restrictive.

The subjective nature of the ratings and their lack of precise equivalence should always be kept uppermost in mind. The true picture of ecologic occurrence, again it should be stressed, is, to the best of our abilities, portrayed individually by species in the descriptions of habitat in our earlier work (Grinnell and Miller, *op. cit.*); some habitat accounts of the water birds in that compilation do not fully define or distinguish breeding habitat for species known in the state primarily as winter visitants. These considerations make it particularly clear that ratings of habitat occurrence should not be subjected to elaborate statistical treatment; the basic data are not sufficiently refined for that purpose. Actual population counts are not usually available, and need of much precise census work in the future is indicated.

In reviewing lists of habitat preferences one must also bear in mind that a formation not listed for a species in California because of only slight or occasional occupancy might elsewhere in the general range of the species, particularly at its margins, be the sole available habitat and hence would locally appear to be the primary habitat. The converse is, of course, true for species occurring rarely or marginally in California. Also, within the area here concerned we find, as in the savannah sparrow (*Passerculus sandwichensis*), some races which occupy one

formation primarily or exclusively, whereas others in different geographic areas must occupy, or by preference occupy, chiefly another of the major ecologic formations; the races may be especially adapted to these differences or may be reacting merely to local availability of habitats. As with zones, it has seemed best to deal solely in species units and designate as the habitat of first consequence, as for the savannah sparrow, the one that has the greatest density of population or, if this is not decisive, the one with the greatest area. Formations supporting endemic or mainly endemic races, yet which are not judged to be of first importance for the species as a whole, are specially annotated.

A relationship score was devised to show something of the affinity of one formation to another with respect to their significance to birds. Thereby also is shown one facet of the relations of one whole community to another. The scores listed and commented on in detail beyond also enter into the general description and appraisal of each formation. They were derived as follows from the species which occurred in from two to five formations; those occurring in more were few and of doubtful significance in reflecting relations of formations. Each species in a given formation was registered as reflecting an affinity for another formation of 0.50 if it occurred in one additional formation; if it occurred in two other formations, it scored an affinity for each of 0.33; if in three other formations, 0.25 each; if in four other formations, 0.20 each. These scores were then summated to show total affinity of any two formations. For example, between oak woodland and desert scrub there are affinities of 0.20 scored by the screech owl, which occurs in these formations among five others; 0.20 for the ash-throated flycatcher, similarly; and 0.50 for the phainopepla, which is listed for these two formations only. The total score is 0.90. For oak woodland and piñon-juniper woodland the total score is 4.26, based on 17 species occurring in both formations.

The formations with symbols adopted for them are as follows:

DS	Desert scrub	}	Scrub group
SB	Sagebrush		
Ch	Chaparral		
PJ	Piñon-juniper woodland	}	Woodland group
OW	Oak woodland		
RW	Riparian woodland		
Sav	Savanna	}	Grassland group
Gr	Grassland		
AM	Alpine meadow		
CF	Coastal forest	}	Coniferous forest group
MF	Montane forest		
SAF	Subalpine forest		
G.IC	Inland cliffs	}	Geologic group
G.SC	Sea cliffs		
G.SS	Seashore		
Ma.F	Fresh-water marsh	}	Marsh group
Ma.S	Salt-water marsh		
W.Lac.	Lacustrine waters	}	Aquatic group
W.Fl.	Fluvial waters		
W.Lit.	Marine littoral waters		
W.Pel.	Pelagic waters		

DESERT SCRUB

Widely spaced, xerophilous plants are the particular feature of this formation (pl. 32a). In stature the larger elements are chiefly 3 to 6 feet high, but small numbers in the aggregate are of species that attain 20 to 25 feet, rarely more. Intervals between the major plants are 10 to 30 feet, and these intervals are largely of bare ground or are covered with transitory, often sparse, forbs. Sparse grasses may occur but are usually local, often marginal, to the formation and scarcely are prominent enough to warrant designating the scrub and grass mixture as a savanna. Rainfall is from 1 to 12 inches annually, usually 5 to 10 inches. The formation as employed here is essentially the same as Clements' (1920:162) "desert scrub."

The most extensive association in California is that of the creosote bush (*Larrea*). Some other larger plants included in the formation or dominating particular associations are mesquite (*Prosopis*), catclaw (*Acacia*), palo verde (*Cercidium*), smoke tree (*Parosela*), desert willow (*Chilopsis*), and desert ironwood (*Olneya tesota*), especially along drainage systems; agaves, nonarborescent yuccas, cholla cactuses, ephedras, and ocotillo (*Fouquieria*) on mesas; saguaro cactus (*Cereus*) in but one small area in California; atriplexes (notably *Atriplex polycarpa*) in margins of desert sinks and in piedmont belts.

Geographically the formation is confined mainly to areas in the state east of the desert divides where it ranges northward in the lower levels of the Mojave Desert and to parts of southern Inyo County. Disconnectedly it occurs in the floor of the southern San Joaquin Valley principally as the atriplex association, but also less extensively as mesquite scrub. The northern limits of the formation are in Fresno County in the Great Valley. In coastal southern California some gravel-strewn arroyos, dotted with cactuses and widely spaced bushes, would seem to fall in the desert scrub formation.

Zonally, the formation lies entirely within the Lower Sonoran, falling short of the upper or northern limits of that zone in many areas.

The birds occurring in the formation are of moderate number (40), with a fairly large (42 per cent) group restricted to it or showing first preference for it. The affinities to other formations (fig. 1) reflected by the birds are diversified although not numerous. Riparian woodland stands highest, evidently because of the combination of desert terrain and climate with water or shade facilities which a number of species seem to require. Relationship with chaparral and sagebrush is strong, doubtless due to broad similarities in the growth form of the plants in these formations. Piñon-juniper woodland stands close because of the transitional Joshua tree belt which is included with it and because of climatic similarities and the frequent mixture of piñon-juniper woodland and scrub which is essential for a number of kinds of birds.

BIRDS OF THE DESERT SCRUB FORMATION

*Turkey Vulture, Sav⁴, OW², Gr², Ch⁴, G.IC², G.SC², SB², RW², PJ²⁰, MF²², CF²², SaF²²

*Swainson Hawk, Sav⁴, Gr², PJ², SB⁴

*Red-tailed Hawk, Sav⁴, OW², Gr², G.IC⁴, RW², Ch², MF², PJ², SB², SaF²²

*Prairie Falcon, G.IC², Gr², SB⁴

- *Sparrow Hawk, Sav¹, OW², Gr³, RW⁴, PJ⁵, G.I.C⁶, MF⁷, S.a.F⁸, SB⁹, CF¹¹
 *Gambel Quail
 *Mourning Dove, Sav¹, OW², RW³, PJ⁵, Gr⁶
 *White winged Dove, RW⁴
 *California Road runner, Ch¹
 *Screech Owl, OW², RW³, PJ⁵, CF⁶
 *Horned Owl, OW², Sav³, G.I.C⁴, RW⁵, MF⁶, CF⁷, S.a.F⁸, PJ⁹, Gr¹⁰, SB¹¹, Ch¹²
 *Elf Owl
 *Burrowing Owl, Gr³
 *Trilling Nighthawk, Gr³
 *Poor-will, SB⁹, Ch¹
 *Costa Hummingbird, Ch¹
 *Gilded Flicker, RW⁴
 *Gila Woodpecker, RW⁴
 *Ladder-backed Woodpecker, PJ⁵, RW⁴
 *Ash-throated Flycatcher, PJ⁵, Ch¹, OW², RW⁴
 *Say Phoebe, G.I.C⁶, Gr³
 *Vermilion Flycatcher, RW⁴
 *Holaretic Raven, G.S.C², G.I.C⁶, Gr³, SB⁹, PJ⁵, Sav¹, S.a.F⁸
 *Verdin
 *Cactus Wren, PJ⁵
 *Mockingbird, Sav¹, PJ⁵
 *Bendire Thrasher
 *LeConte Thrasher
 *California Thrasher, Ch¹
 *Crissal Thrasher, SB⁹
 *Black-tailed Gnatcatcher, Ch¹
 *Phainopepla, OW²
 *Loggerhead Shrike, Sav¹, Gr³, PJ⁵, SB⁹, OW²
 *Lucy Warbler
 *Scott Oriole, PJ⁵
 *House Finch, Sav¹, Gr³, OW², G.I.C⁶, RW⁴, PJ⁵, SB⁹, Ch¹
 *Abert Towhee, RW⁴
 *Lark Sparrow, Sav¹, Gr³, OW², Ch¹, SB⁹
 *Black-throated Sparrow, SB⁹
 *Bell Sparrow, SB⁹, Ch¹

SAGEBRUSH

The essential features of the formation are densely foliated, woody bushes, chiefly 2 to 5 feet high, moderately spaced (pl. 32b). The intervals between the principal plants are such that alleyways 2 to 6 feet wide occur. Thus the open spaces are much less than in the desert scrub formation. Spacing is not so close as in chaparral, which, except marginally, forms an unbroken mass of vegetation. Occasionally sagebrush becomes continuous, but usually only locally. The dominant plants are xerophytic, yet with leaf surface not so extremely reduced as in desert scrub types such as *Acacia* and *Fouquieria*. They occur in areas receiving 5 to 15 inches of annual rainfall.

The dominant plants of the formation are sagebrush (most notably *Artemisia tridentata*), species of rabbit brush (*Chrysothamnus*, particularly *C. nauseosus*), *Atriplex*, *Tetradymia*, and *Sarcobatus*.

Excluded from the sagebrush formation, contrary to Clements' treatment (1920: 150), is the salvia-artemisia association which occurs in coastal southern and cen-

* A ~~type~~ occurs with primary affinity for desert scrub.

tral California. This association, although the most xerophytic of those I have grouped with chaparral, seems from the birds' standpoint to fall better with chaparral than with sagebrush because of its compactness and extensive intermixture with more typical chaparral associations.

Sagebrush formation in the sense here employed is found primarily east of the desert and principal mountain divides and above the floor of the lower deserts and valleys. It is fairly continuous from Inyo County northward and on the mountain slopes bordering the deserts and the Great Basin on the west. Characteristically it mixes with the open coniferous forests of the interior and extends upward irregularly through them to come in contact with alpine meadows. There is considerable invasion of Pacific drainages along the mountain crests and westward into the Pit River and Klamath River systems. Sagebrush also mixes typically with piñon-juniper woodland.

Zonally the formation occurs chiefly in the Upper Sonoran and Transition. The above-mentioned extensions upward through forest belts carry the formation into levels regarded as Canadian or even sometimes as Hudsonian.

The sagebrush formation is not rich in number of bird species, possibly because of its comparative uniformity; 29 species may be listed; 7, or 24 per cent, show primary or exclusive adherence to the formation. The relationship indexes (fig. 1) show a strong affinity with desert scrub, doubtless the result of resemblance in life-form and geographic and climatic affinity. Chaparral, grassland, piñon-juniper, and riparian woodland show lesser affinities; all other affinities are definitely weak. Somewhat surprising is the moderate relation to chaparral in spite of inclusion of the *salvia-artemisia* association with chaparral rather than with sagebrush as advocated on botanical grounds by Clements. The placing of it with chaparral as far as birds are concerned seems supported by this relationship score; evidently the score would be unnaturally increased if Clements' classification were followed.

BIRDS OF THE SAGEBRUSH FORMATION

¹Turkey Vulture, Sav¹, OW², Gr², Ch², G.I.C², G.S.C², RW², DS², P.J.¹⁰, MF¹¹, CF¹², Sa.F¹³

²California Condor, G.I.C¹, Ch², Gr², MF², OW², Sav², P.J.⁷

³Red-tailed Hawk, Sav², OW², Gr², G.I.C², RW², Ch², MF², P.J.², DS¹⁰, Sa.F¹³

⁴Golden Eagle, Sav², OW², G.I.C², MF², Sa.F¹³, P.J.², Ch²

⁵Swanson Hawk, Sav², Gr², P.J.², DS²

¹⁰Sparrow Hawk, Sav², OW², Gr², RW², P.J.², G.I.C², MF², Sa.F¹³, DS², CF¹²

⁶Prairie Falcon, G.I.C¹, Gr², DS²

⁷Sage Grouse

¹¹Horned Owl, OW², Sav², G.I.C², RW², DS², MF², CF¹², Sa.F¹³, P.J.², Gr¹², Ch¹²

⁸Poor-will, Ch², DS²

⁹Gray Flycatcher, P.J.²

¹²Black-billed Magpie, RW²

¹⁴Holarctic Raven, G.S.C², G.I.C², Gr², DS², P.J.², Sav², Sa.F¹³

¹⁵Sage Thrasher

¹⁶Orsinal Thrasher, DS²

¹⁷Mountain Bluebird, Sa.F¹³, AM², MF²

¹⁸Loggerhead Shrike, Sav², Gr², P.J.², DS², OW²

¹⁹Brewer Blackbird, Sav², Gr², OW², CF¹², MF², RW², Ma.F¹⁴, P.J.²

²⁰Brown-headed Cowbird, RW², Gr², OW², P.J.²

²¹House Finch, Sav², DS², Gr², OW², G.I.C², RW², P.J.², Ch²

¹Arkansas Goldfinch, Sav¹, OW², RW³, Ch⁴, Gr⁵, CF⁶, PJ⁷

²Green-tailed Towhee, Ch¹

³Spotted Towhee, Ch¹, RW², CF⁴, OW⁵, PJ⁶

⁴Vesper Sparrow

⁵Lark Sparrow, Sav¹, Gr², OW³, Ch⁴, DS⁵

⁶Black-throated Sparrow, DS¹

⁷Bell Sparrow, Ch², DS¹

⁸Brewer Sparrow

⁹Black-chinned Sparrow, Ch¹

CHAPARRAL

A great variety of plants in California develop the form of chaparral. The common characteristic of significance for birds is the close proximity of plant units so that large clumps or tracts of foliage or tangled branchwork occur without discontinuity at the upper levels and this at heights of 2 to 8 feet above the ground (pl. 33a). Beneath are covered alleyways and abundant ground litter. The typical compactness of the formation may be broken by intrusion of grassy areas, trees, or rock formations; but uncovered lanes between separate bushes are few. The plants vary from moderately xerophilous types to broad-leaved species requiring much atmospheric humidity, as provided in the northern coastal fog belt. Rainfall ranges from 10 to 60 inches.

Such a formation, it may be noted, may be a climax growth or subclimax, as, for example, the montane chaparral in succession of forest recovery. Again we may stress that for the bird the plant cover is just as suitable as a chaparral habitat whether or not it is to be replaced eventually by coniferous trees. The concept here outlined is more inclusive, then, than that of Clements' chaparral climax (1920:177ff.), which is dominated by *Quercus*, *Ceanothus*, and *Adenostoma*. To exemplify the scope of our category the following plant components may be mentioned: *Artemisia californica*, *Salvia mellifera*, *Salvia apiana*, *Eriogonum fasciculatum*, *Eriodictyon*, *Quercus dumosa*, *Cercocarpus*, *Ceanothus*, *Arctostaphylos*, *Adenostoma*, *Rhamnus*, *Prunus*, *Rhus*, bush lupines (*Lupinus*), *Baccharis pilularis*, *Symphoricarpos*, *Ribes*, *Holodiscus*, *Vaccinium*, *Physocarpus capitatus*, *Gaultheria shallon*, *Corylus rostrata*, and *Acer circinatum*. Some of these occur also quite as typically as forest understory, but in exposed situations they take on the form of chaparral.

The chaparral of California can be grouped into the following intergrading subdivisions: (1) coastal sage; (2) typical dry or hard chaparral; (3) humid or soft chaparral; (4) subclimax brush of the coastal forest; and (5) subclimax brush of the montane and lower subalpine forests.

Definitely excluded are true forest and woodland understory which is shaded by the trees and hence usually much less compact than chaparral. Also excluded are streamside tangles, which are viewed as part of riparian woodland, and weedy and marshy tangles or plants of more purely vertical growth form such as nettles (*Urtica*).

Chaparral is found chiefly west of the divides separating the deserts and the Great Basin from the coastal drainage. On mountain spurs extending to the eastward, as the Santa Rosa Mountains and the Little San Bernardino Mountains, there

* A race occurs with primary affinity for sagebrush.

is much chaparral. The isolated ranges farther eastward develop limited tracts of *Cercocarpus*, or of *Purshia* and compact *Artemisia*, or, at higher levels, subclimax chaparral in the forest belt, as on the Warner Mountains. The largest developments of the formation are in the hills and mountains of coastal southern California and the central Coast Ranges and in the hills bordering the Great Valley.

The zonal range is broad, extending from the Lower Sonoran, marginally, on the southern coast, up to the lower Canadian of the mountains. But chaparral is developed predominantly in the Upper Sonoran, with secondary yet extensive areas in the Transition Zone.

The number of species of birds (43) found in chaparral is not conspicuously large considering the diversity of plant components and of temperature and humidity within this broad category. The essential constancy in growth form of the chaparral is doubtless an appreciable factor in holding down the number. The number might be almost as low as for sagebrush were it not for the aforementioned diversity. Species with primary or exclusive adherence to chaparral comprise 20, or 46 per cent, a high proportion for a terrestrial formation, and conspicuously greater than that for sagebrush. Affinities with other formations are low and diversified (fig. 1). Riparian woodland, oak woodland, and desert scrub are of about equal rank, with piñon-juniper, grassland, sagebrush, and montane forest not far below. All these except desert scrub and sagebrush are considerably intermixed with chaparral in many sections; this factor, through combined usage, accounts in large part for their relationship scores and the absence of one principal affinity. The position of sagebrush is unexpectedly low in the series. This results chiefly from the disparity of sizes of the avifaunas of the two; the additional species of the chaparral strengthen somewhat the bonds with other intermixed formations.

BIRDS OF THE CHAPARRAL FORMATION

¹Turkey Vulture, Sav¹, OW², Gr³, G.I.C⁵, G.S.C⁶, SB⁷, RW⁸, DS⁹, PJ¹⁰, MF¹¹, CF¹², SaF¹³

²California Condor, G.I.C¹, Gr², MF⁴, OW³, Sav⁵, PJ⁷, SB⁸

³Red-tailed Hawk, Sav¹, OW², Gr³, G.I.C⁴, RW⁵, MF⁷, PJ⁸, SB⁹, DS¹⁰, SaF¹¹

⁴Golden Eagle, Sav¹, OW², Gr³, G.I.C⁴, MF⁵, SaF⁶, PJ⁷, SB⁸

⁵Mountain Quail, OW¹, MF², CF³, PJ⁴

⁶California Quail, Gr¹

⁷California Road-runner, DS¹

⁸Horned Owl, OW¹, Sav², G.I.C³, RW⁴, MF⁵, CF⁶, SaF⁷, PJ⁸, Gr⁹, SB¹⁰

⁹Poor-will, SB¹, DS²

¹⁰Costa Hummingbird, DS¹

¹¹Anna Hummingbird, OW¹

¹²Broad-tailed Hummingbird, PJ¹

¹³Allen Hummingbird, CF¹

¹⁴Ash-throated Flycatcher, PJ¹, OW², DS³, RW⁴

¹⁵Wright Flycatcher, SaF¹, MF²

¹⁶Scrub Jay, OW¹, PJ²

¹⁷Bush-tit, OW¹, PJ², RW³

¹⁸Wren-tit

¹⁹House Wren, OW¹, RW², MF³, CF⁴, SaF⁵

²⁰Bewick Wren, PJ¹, RW², OW³

²¹California Thrasher, DS¹

* A race occurs with primary affinity for chaparral.

- ¹Blue-gray Gnatcatcher, OW¹, PJ², RW⁴
²Black-tailed Gnatcatcher, DS¹
³Gray Vireo, PJ¹
⁴Orange-crowned Warbler, OW², RW³, CF⁴, SaF⁵, MF⁶
⁵Nashville Warbler, MF³, OW¹
⁶Tolmie Warbler, RW¹, CF³, MF⁴, SaF⁵
⁷Pileolated Warbler, RW¹, CF³, SaF⁴
⁸Lazuli Bunting, Gr², RW³
⁹House Finch, Sav¹, DS², Gr³, OW⁴, G.I.C⁵, RW⁶, PJ⁷, SB⁸
¹⁰American Goldfinch, RW¹, Gr²
¹¹Arkansas Goldfinch, Sav¹, OW², RW³, Gr⁴, CF⁵, PJ⁶, SB⁷
¹²Lawrence Goldfinch, OW¹, MF², Gr³
¹³Green-tailed Towhee, SB¹
¹⁴Spotted Towhee, RW², SB³, CF⁴, OW⁵, PJ⁶
¹⁵Brown Towhee, OW², RW³
¹⁶Lark Sparrow, Sav¹, Gr², OW³, DS⁴, SB⁵
¹⁷Rufous-crowned Sparrow, Gr²
¹⁸Bell Sparrow, SB¹, DS²
¹⁹Black-chinned Sparrow, SB¹
²⁰White-crowned Sparrow, Gr², AM³
²¹Fox Sparrow, RW²
²²Song Sparrow, RW¹, Ma.F², Ma.S⁴

PIÑON-JUNIPER WOODLAND

Piñon-juniper woodland is an open formation in which there is always much intermixed xerophilous brush, usually derived from the sagebrush formation (pl. 33b). Grass is but slightly developed in the intervals. This circumstance and the frequently precipitous terrain on which the formation develops distinguish it from savanna as here conceived, although there are many features in common. The trees are of small stature (15-35 feet) and the branches seldom interlock because of the spacing. Scant needle duff accumulates and low green forbs are rare in the limited shade beneath the trees. Foliage is rigid and nondeciduous, since the trees are either conifers or arborescent yuccas. Strong seasonal contrasts prevail in the area of the formation, and rainfall is low—10 to 20 inches. Although both in openness and stature the typical piñon association resembles other western woodlands, the trees themselves tend to relate the assemblage to coniferous forests. The secondary Joshua tree association, on the other hand, because of the extreme openness of its growth, has strong affinities with desert scrub and savanna; it is usually found on level or moderately sloping terrain. It seems best to group it with the piñon-juniper formation rather than with the oak-pine woodland, as Clements (1920:204) has done.

The dominant tree species are *Pinus monophylla*, *Juniperus californica*, and *Yucca brevifolia*. The first two are frequently mixed, although pure stands of each may occur. Intermixture of yucca and the conifers is found usually in a restricted zone between vertically complementary yucca and piñon belts. Widely scattered yuccas or junipers, 100 or more feet apart, would not be regarded as constituting this formation. Occasional dense stands of piñons may actually take on the aspects of coniferous forest.

* A race occurs with primary affinity for chaparral.

The piñon-juniper formation occurs on the east side of the Sierra Nevada-Cascade axis, broadly on the Modoc plateau and again in the Inyo and Mojave Desert areas. Southward it stops short of the Colorado River and the Imperial and Coachella valleys, but it rims the deserts to the west on the arid slopes of the mountains. Extensions westward in the Tehachapi district are considerable; and here,

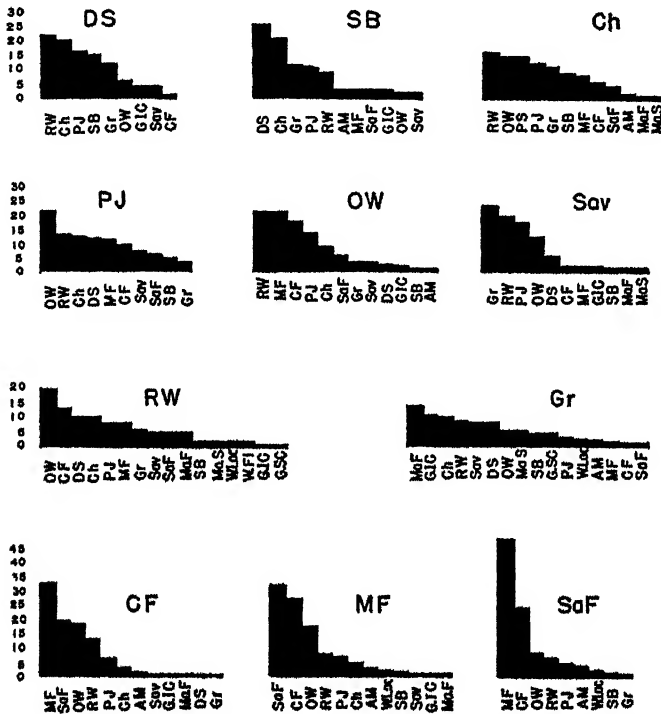


Fig. 1. Relationship scores for ecologic formations based on occurrences of birds. Scores for each formation (see p. 542 and table 5) are here expressed as percentages (heights of columns) of total of scores relating that formation to other ecologic categories.

as in mountains farther south, there is contact with the related oak woodlands of drier types.

Zonally the formation is Upper Sonoran, except for the Joshua tree association, which is Lower Sonoran. Local conditions of slope and soil occasionally carry the piñons upward on the eastern escarpment of the Sierra Nevada to levels normally regarded as Transition or even Canadian.

Piñon-juniper attracts 45 species of birds, but only 4, or 9 per cent, show exclusive or principal preference for it. One reason for this low number of principal adherents is the close relationship of the formation with oak woodland. Most species occurring in both are rated first for oak woodland because population densities often seem to be greater in it. However, it is to be noted that piñon-juniper harbors a total of six geographic races which, although they are sub-

divisions of species with other principal affinities, show first adherence to the piñon association. Thus the percentage of principal adherents is not an accurate reflection of the importance of the formation as a habitat, although, in comparison with oak woodland, piñon-juniper admittedly is an impoverished avian habitat.

Affinities of piñon-juniper woodland are fairly diversified, although strong affinity for oak woodland is shown (fig. 1). Riparian woodland, chaparral, desert scrub, the lower coniferous forests, and savanna are of secondary but, among themselves, more or less equivalent relationship. The definite entrance of coniferous forest into the relationships is significant as a reflection of the botanical affinity of the dominant plants and its effect on bird life despite the open aspect of the formation.

BIRDS OF THE PIÑON-JUNIPER FORMATION

¹⁰Turkey Vulture, Sav¹, OW², Gr¹, Ch¹, G.I.C³, G.S.C³, SB³, RW³, DS³, MF¹¹, CF¹², SaF¹³

¹¹California Condor, G.I.C¹, Ch¹, Gr¹, MF¹, OW¹, Sav², SB²

¹²Cooper Hawk, RW¹, OW², MF³, CF³

¹³Red-tailed Hawk, Sav¹, OW², Gr¹, G.I.C⁴, RW⁵, Ch⁴, MF⁷, SB⁸, DS¹⁰, SaF¹¹

¹⁴Swainson Hawk, Sav¹, Gr², SB⁴, DS⁵

¹⁵Golden Eagle, Sav¹, OW², Gr², G.I.C⁴, MF⁵, SaF⁶, Ch⁸, SB⁹

¹⁶Sparrow Hawk, Sav¹, OW², Gr¹, RW⁴, G.I.C⁵, MF⁷, SaF⁸, DS⁹, SB¹⁰, CF¹¹

¹⁷Mountain Quail, Ch¹, OW², MF³, CF⁴

¹⁸Mourning Dove, Sav¹, OW², RW³, DS⁴, Gr⁵

¹⁹Screech Owl, OW¹, RW², DS³, CF³

²⁰Horned Owl, OW¹, Sav², G.I.C³, RW⁴, DS⁵, MF⁶, CF⁷, SaF⁸, Gr¹⁰, SB¹¹, Ch¹²

²¹Pigmy Owl, CF¹, MF², OW³

²²Long-eared Owl, RW¹, OW²

²³Broad-tailed Hummingbird, Ch¹

²⁴Red-shafted Flicker, RW¹, MF², OW³, CF⁴, SaF⁵

²⁵Hairy Woodpecker, MF¹, SaF², CF³, RW⁴

²⁶Ladder-backed Woodpecker, DS¹, RW²

²⁷Western Kingbird, Sav¹, Gr²

²⁸Cassin Kingbird, Sav¹

²⁹Ash-throated Flycatcher, Ch¹, OW², DS⁴, RW⁵

³⁰Gray Flycatcher, SB¹

³¹Scrub Jay, OW¹, Ch²

³²Holarctic Raven, G.S.C¹, G.I.C², Gr³, DS⁴, SB⁵, Sav⁷, SaF⁸

³³Pinon Jay

³⁴Mountain Chickadee, SaF¹, MF²

³⁵Plain Titmouse, OW¹

³⁶Bush-tit, OW¹, Ch², RW⁴

³⁷White-breasted Nuthatch, MF¹, OW², SaF³

³⁸Bewick Wren, Ch¹, RW², OW⁴

³⁹Cactus Wren, DS¹

⁴⁰Mockingbird, Sav¹, DS²

⁴¹Mexican Bluebird, OW¹, MF², Sav³, Gr⁴, RW⁵, CF⁶, SaF⁸

⁴²Blue-gray Gnatcatcher, OW¹, Ch², RW⁴

⁴³Loggerhead Shrike, Sav¹, Gr², DS⁴, SB⁵, OW⁶

⁴⁴Gray Vireo, Ch¹

⁴⁵Black-throated Gray Warbler, OW¹, CF², MF⁴

⁴⁶Scott Oriole, DS¹

⁴⁷Brewer Blackbird, Sav¹, Gr², OW³, CF⁴, MF⁵, RW⁶, Ma.F⁷, SB⁸

⁴⁸Brown-headed Cowbird, RW¹, Gr², SB³, OW⁴

* A race occurs with primary affinity for piñon-juniper woodland.

^aWestern Tanager, MF¹, SaF², CF¹, OW⁴

^bBlack-headed Grosbeak, RW¹, OW², MF³, CF⁴

^cHouse Finch, Sav¹, DS², Gr³, OW⁴, GIC⁵, RW⁶, SB⁷, Ch⁸

^dArkansas Goldfinch, Sav¹, OW², RW³, Ch⁴, Gr⁵, CF⁶, SB⁷

^eSpotted Towhee, Ch¹, RW², SB³, CF⁴, OW⁵

^fChipping Sparrow, MF¹, SaF², OW³, CF⁴

(OAK WOODLAND

The trees of oak woodland in California are close enough together so that many of them touch branches; yet characteristically this continuity is limited, connecting several members of a clump or a row of trees along a canyon bench (pl. 34a). There are many gaps 20 to 50 feet wide which usually are either grass-covered or grown to brush. Continuity is locally better than in the piñon-juniper formation, and intervals are more often grassy or grown to forbs near or under the broad-leaved trees. The oaks range chiefly from 20 to 50 feet in height; *Quercus lobata* is an exception, with consistently greater height when mature. Beside oaks, Digger pines and some other Upper Sonoran conifers growing in scattered fashion are part of the formation; madrone is a frequent element; big-leaf maple is a member of the less xeric association. Rainfall ranges from 15 to 30 inches, occasionally higher.

The principal subdivisions of this formation are: (1) the live oak association (*Quercus agrifolia*, *Q. wislizenii*, *Q. engelmannii*), which southerly and interiorly is the most xeric of the associations and is frequently mixed with chaparral formation; (2) the valley oak association (*Quercus lobata*), most frequently merging into savanna and normally with grass in the intervals between trees; (3) the blue oak—Digger pine association (*Quercus douglasii*, *Pinus sabiniana*), commonly intermingled with grass but also frequently with interspersed clumps of manzanita-dominated chaparral; (4) the golden oak association (*Quercus chrysolepis*), seldom extensive and developed chiefly in canyons and on shaded slopes; the oak is frequently of chaparral stature and often grades from a montane chaparral into woodland; madrone may be associated; (5) the Garry oak association (*Quercus garryana*), appearing as small tracts of woodland in the less humid parts of the coastal forest belt and somewhat interiorly in part of the area of montane forest; thus it is usually in contact with coniferous forest and may mix with it, although this is true less than with the black oak and the tan oak; grass and montane chaparral occur beneath and around the trees; (6) the black oak association (*Quercus kelloggii*), seldom forming a true woodland but occurring as a member of the lower montane forest, particularly in combination with yellow pine; however, benches and dry valley floors in the mountains may develop black oaks in pure stand, and on some slopes this oak with maple and madrone forms a broad-leaved woodland.

The tan oak (*Lithocarpus densiflora*) is best regarded as an element in the coastal forest; yet perhaps only slightly less than the black oak it forms small tracts of woodland. However, in compactness of foliage mass and denseness of stand the tan oaks are related to the forest formation more than to the spreading broad-leaved woodlands which other oaks effect.

The oak woodlands herein described are more inclusive than Clements' pine-oak woodland, which would seem to be chiefly the blue oak—Digger pine and live oak associations of our grouping. These are, of course, the most conspicuous oak associations in the state.

This diverse formation occurs with unimportant exception west of the Sierran-Cascade divides, the whole length of the state. It extends to the coast, although it is scarce on actual seaward exposures and is all but absent in the very humid narrow coastal strip of the northwest.

The zonal range is Upper Sonoran and Transition.

A large avifauna inhabits oak woodland—63 species. Both the interspersions with grassland, chaparral, and coniferous forest formations and the diversity of oak types and the correlated climates are underlying causes. The uniformity and distinctiveness of the formation for birds is less than that for chaparral; hence the number of species is greater, but the proportion of exclusive and principal adherents is less—16, or 24 per cent.

The oak woodland avifauna shows moderately strong relations with several formations (fig. 1), yet the relationships are not so widely diversified as are those of the piñon-juniper and chaparral formations. Riparian woodland, montane forest, and coastal forest are of similar high rank. All are much interspersed with oak woodland and possess the common element of trees of considerable stature. Riparian woodland has also in common the broad-leaved character of the trees, which has much bearing on the presence or absence of some species of birds. The prevailingly harsher foliage of the oak woodland is, on the other hand, a contrasting factor. Piñon-juniper and chaparral show progressively lower relationship scores, but their low scores are in one sense artificial because of their smaller avifaunas relative to those of riparian woodland and montane and coastal forests. The reciprocal relationships show that the highest percentages of affinity of both chaparral and piñon-juniper are with oak woodland. The disparity in size of avifaunas is, however, one sign of distinctness and hence of lack of relationship.

BIRDS OF THE OAK WOODLAND FORMATION

*Turkey Vulture, Sav⁴, Gr⁴, Ch⁴, G.I.O⁴, G.S.C⁴, SB⁴, RW⁴, DS⁴, P.J.¹⁰, MF¹¹, CF¹², Sa.F¹³

*California Condor, G.I.O⁴, Ch⁴, Gr⁴, MF⁴, Sav⁴, P.J.¹, SB⁴

*Cooper Hawk, RW⁴, MF⁴, P.J.⁴, CF¹²

*Sharp-shinned Hawk, MF⁴, CF¹²

*Red-tailed Hawk, Sav⁴, Gr⁴, G.I.O⁴, RW⁴, Ch⁴, MF⁴, P.J.⁴, SB⁴, DS¹⁰, Sa.F¹¹

*Golden Eagle, Sav⁴, Gr⁴, G.I.O⁴, MF⁴, Sa.F¹¹, P.J.⁴, Ch⁴, SB⁴

*Sparrow Hawk, Sav⁴, Gr⁴, RW⁴, P.J.⁴, G.I.O⁴, MF⁴, Sa.F¹¹, DS⁴, SB¹⁰, CF¹²

*Mountain Quail, Ch⁴, MF⁴, CF⁴, P.J.⁴

*Band-tailed Pigeon, MF⁴, CF⁴

*Mourning Dove, Sav⁴, RW⁴, DS⁴, P.J.⁴, Gr⁴

*Barn Owl, G.I.O⁴, Gr⁴, Sav⁴

*Screech Owl, RW⁴, DS⁴, P.J.⁴, CF¹²

*Horned Owl, Sav⁴, G.I.O⁴, RW⁴, DS⁴, MF⁴, CF¹², Sa.F¹¹, P.J.⁴, Gr¹⁰, SB¹¹, Ch¹³

*Pigmy Owl, CF⁴, MF⁴, P.J.⁴

*Spotted Owl, CF⁴, MF⁴

*Long-eared Owl, RW⁴, P.J.⁴

*Say-whet Owl, MF⁴, Sa.F¹¹

*Black-chinned Hummingbird, RW⁴

- ²Anna Hummingbird, Ch¹
- ²Red-shafted Flicker, RW¹, MF⁴, CF⁴, SaF⁵, PJ⁶
- ¹Acorn Woodpecker, MF¹, CF¹
- ¹Lewis Woodpecker, MF²
- ¹Downy Woodpecker, RW¹, CF²
- ¹Nuttall Woodpecker, RW¹
- ²Ash-throated Flycatcher, PJ¹, Ch⁴, DS⁴, RW²
- ⁴Western Flycatcher, CF², RW², MF²
- ²Western Wood Pewee, MF², SaF², RW⁴, CF⁵
- ⁴Violet-green Swallow, MF², G.I.C⁴, CF²
- ²Purple Martin, CF¹, MF¹, Sav¹
- ⁴Stellar Jay, MF¹, CF², SaF², RW²
- ¹Scrub Jay, Ch¹, PJ²
- ²Yellow-billed Magpie, Sav¹, Gr², RW⁴
- ²American Crow, RW¹, Sav⁴, Gr⁴, CF⁵, G.SS⁵
- ²Chestnut-backed Chickadee, CF², RW¹
- ¹Plain Titmouse, PJ¹
- ¹Bush-tit, PJ², Ch², RW⁴
- ²White-breasted Nuthatch, MF¹, SaF², PJ⁴
- ¹House Wren, RW¹, MF¹, CF⁴, SaF², Ch²
- ⁴Bewick Wren, Ch¹, PJ², RW²
- ¹Mexican Bluebird, MF², Sav², Gr⁴, RW², CF², PJ¹, SaF²
- ¹Blue-gray Gnatcatcher, PJ¹, Ch², RW⁴
- ²Phainopepla, DS¹
- ²Loggerhead Shrike, Sav¹, Gr², PJ¹, DS⁴, SB²
- ¹Hutton Vireo, CF², RW²
- ²Solitary Vireo, MF¹, RW²
- ²Warbling Vireo, RW¹, SaF²
- ²Orange-crowned Warbler, Ch¹, RW², CF⁴, SaF², MF²
- ¹Nashville Warbler, MF¹, Ch²
- ¹Black-throated Gray Warbler, PJ², CF², MF⁴
- ²Bullock Oriole, RW¹, Sav², Gr⁴
- ²Brewer Blackbird, Sav¹, Gr², CF⁴, MF², RW², Ma.F², SB⁴, PJ²
- ⁴Brown-headed Cowbird, RW¹, Gr², SB², PJ²
- ⁴Western Tanager, MF², SaF², CF², PJ²
- ²Black-headed Grosbeak, RW¹, MF², CF⁴, PJ²
- ²Purple Finch, CF¹, MF², RW⁴
- ⁴House Finch, Sav¹, DS², Gr², G.I.C², RW², PJ¹, SD², Ch²
- ²Arkansas Goldfinch, Sav¹, RW², Ch⁴, Gr², CF², PJ¹, SB²
- ¹Lawrence Goldfinch, MF², Gr², Ch⁴
- ²Spotted Towhee, Ch¹, RW², SB², CF¹, PJ²
- ²Brown Towhee, Ch¹, RW²
- ²Lark Sparrow, Sav¹, Gr², Ch⁴, DS², SB²
- ²Oregon Junco, SaF², MF², CF², AM⁴
- ²Chipping Sparrow, MF¹, SaF², PJ⁴, CF²

RIPARIAN WOODLAND

This formation consists of broad-leaved deciduous trees growing on bottom lands near streams or where there is good subsurface water supply (pl. 34b). Typically, it is compact woodland, but it may consist of tree rows or substantial tree clumps more extensive and closely set than in savannas. Sycamores forming riparian woodland in arroyos are characteristically well spaced. In height the trees vary from 15 to 100 feet. For birds this woodland in the West is the most lush type available, the least xeric of the strictly terrestrial formations. The predominance

of light green foliage and the usual presence of exposed water sources are significant features for birds.

This formation includes always a high proportion of "edge" situation; it is of course seral in terms of successional ecology. In the Transition Zone the interdigitation with and diffusion into other formations is conspicuous, but in Lower Sonoran areas the borders of riparian woodland normally are sharp.

A variety of situations is grouped under riparian woodland. Willows (*Salix*), Fremont and black cottonwoods (*Populus fremontii*, *P. trichocarpa*), and white and red alders (*Alnus rhombifolia*, *A. rubra*) are the most widespread and important dominants. Less extensive or less typical participants are western sycamores (*Platanus racemosa*) and fan palms (*Washingtonia filifera*). California laurel (*Umbellularia californica*) and aspen (*Populus tremuloides*) may form woodland along streams and then properly are regarded as riparian. However, these trees would not be so classed in other situations, for example when they are intermixed elements in coastal and subalpine forests. Associated with the trees of riparian woodland are understory and marginal brush and vine tangles. Typical are blackberry, wild grape, nettles, *Artemisia vulgaris*, wild rose, and creek dogwood.

Excluded from the formation are mountain meadows with scattered low willow bushes, aspen thickets on steep slopes where there is no appreciable stream development, and dry brush along arroyos.

The formation occurs locally in all sections of the state, but it is of course very sparse in the southeastern desert areas and is little developed in the higher mountains. Zonally it ranges from Lower Sonoran to Canadian. The climatic characteristics of riparian woodland areas in the Colorado River valley and in the Canadian Zone of the Sierra Nevada are strikingly different, yet through the factor of water supply a fundamentally similar tree growth is supported, the common growth-form features of which support a few species of birds throughout the zonal range. A notable example is the yellow warbler. Other species are sharply limited within the range of the formation by temperature differences, as for example the Bell vireo and fox sparrows.

The number of species of birds associated with riparian woodland is larger than that of any other formation. The total of 75 is approached closely only by montane forest. Also, the number with primary affinity is large, 33, although in terms of percentage (44) this group is not the greatest. One may note several factors which operate to cause these large totals. Great zonal range is undoubtedly one. A second is the high development of "edge" situation in contact with a variety of other formations. A third is a fundamental similarity in life-form to the eastern broad-leaved woodlands or forests with their rich avifauna. In California, with large, prevailingly xeric or semixerix areas and plant formations, riparian woodland, although areally insignificant, is the chief suitable habitat for a large avifauna, widespread elsewhere, that depends on broad-leaved deciduous forests or woods with good summertime shade and available surface water.

The affinity scores for riparian woodland are extremely diverse (fig. 1), owing to multiple contacts with other formations in the course of the wide zonal range. The situation is comparable to that of grassland. Affinity with oak woodland is

greatest because of some fundamental likenesses in growth form and extensive contact. Relation to coastal forest is fairly high, probably because of development of streams in the general area of this forest, which lies at low elevations in a well-watered district. There is the common dependence of the two on moisture, although in different degree and form, and this is reflected in diffusion through both of some of the same tree species. Consequently, for birds there are certain significant resemblances in growth form, at least among subdominants.

The fairly high relationship to desert scrub is puzzling until one notes a considerable number of low-zone, desert-dwelling species which are restricted to areas where water and shade are available. These are obliged to make use of both riparian and desert scrub situations in carrying on their full range of activities.

BIRDS OF THE RIPARIAN WOODLAND FORMATION

- ^aGreen Heron, W.Fl.¹, W.Lac.-
- ^aWood Duck, W.Fl.¹, W.Lac.^a
- ^aTurkey Vulture, Sav¹, OW¹ Gr¹, Ch¹, G.IC^a, G.SC^a, SB¹, DS^a, PJ¹⁰, MF¹¹, CF¹⁴, SaF¹⁴
- ¹White-tailed Kite, Ma.F^a, Sav¹, Gr¹, Ma.S¹
- ¹Cooper Hawk, OW^a, MF^a, PJ^a, CF^a
- ^aRed-tailed Hawk, Sav¹, OW¹, G.I¹, G.IC^a, Ch^a, MT¹⁰, PJ^a, SB¹⁰, DS¹⁰, SaF¹¹
- ¹Red-shouldered Hawk
- ¹Harris Hawk
- ^aSparrow Hawk, Sav¹, OW^a, Gr^a, PJ^a, G.IC^a, MF^a, SaF^a, DS^a, SB¹⁰, CF¹⁴
- ¹Ruffed Grouse
- ¹Mourning Dove, Sav¹, OW^a, DS^a, PJ^a, Gr^a
- ^aWhite-winged Dove, DS¹
- ¹Ground Dove
- ¹Yellow-billed Cuckoo
- ^aScreech Owl, OW¹, DS^a, PJ^a, CF^a
- ^aHorned Owl, OW¹, Sav^a, G.IC^a, DS^a, MF^a, CF^a, SaF^a, I.P¹⁰, Gr¹⁰, SB¹¹, Ch¹²
- ¹Long-eared Owl, OW^a, PJ^a
- ¹Black-chinned Hummingbird, OW^a
- ¹Red-shafted Flicker, MF^a, OW^a, CF^a, SaF^a, PJ^a
- ^aGilded Flicker, DS¹
- ^aGila Woodpecker, DS^a
- ^aYellow-bellied Sapsucker, MF¹¹, SaF¹⁴, CF¹⁴
- ^aHairy Woodpecker, MF¹¹, SaF¹⁴, CF¹⁴, PJ^a
- ¹Downy Woodpecker, OW^a, CF^a
- ^aNuttall Woodpecker, OW¹
- ^aLadder-backed Woodpecker, PJ¹, DS^a
- ^aEastern Kingbird, Sav¹, Gr¹
- ^aAsh-throated Flycatcher, PJ¹, Ch^a, OW^a, DS^a
- ^aBlack Phoebe, G.IC¹, G.SC^a
- ¹Trail Flycatcher
- ^aWestern Flycatcher, CF^a, MF^a, OW^a
- ^aWestern Wood Pewee, MF¹¹, SaF¹⁴, OW^a, CF^a
- ^aVermilion Flycatcher, DS¹
- ¹Tree Swallow, Ma.F^a, CF^a, MF^a
- ^aStellar Jay, MF¹¹, CF^a, SaF¹⁴, OW^a
- ¹Black-billed Magpie, SB^a
- ^aYellow-billed Magpie, Sav¹, OW^a, Gr^a
- ¹American Crow, OW^a, Sav^a, Gr^a, CF^a, G.SS^a
- ¹Black-capped Chickadee
- ^aChestnut-backed Chickadee, CF^a, OW^a

- ⁴Bush-tit, OW², PJ¹, Ch⁴
- ²House Wren, OW¹, MF⁴, CF⁴, SaF⁶, Ch⁶
- ¹Bewick Wren, Ch¹, PJ², OW⁴
- ⁶Robin, MF¹, Gr², SaF³, CF⁴, AM²
- ¹Swainson Thrush, CF²
- ²Mexican Bluebird, OW¹, MF³, Sav³, Gr⁴, CF⁶, PJ¹, SaF⁶
- ⁴Blue-gray Gnatcatcher, OW¹, PJ³, Ch⁴
- ¹Hutton Vireo, OW¹, CF²
- ¹Bell Vireo
- ¹Solitary Vireo, MF², OW¹
- ¹Warbling Vireo, OW², SaF⁶
- ¹Orange-crowned Warbler, Ch¹, OW², CF⁴, SaF³, MF⁶
- ¹Yellow Warbler
- ¹Tolmie Warbler, Ch¹, CF⁴, MF⁴, SaF³
- ¹Yellow-throat, Ma.F¹, Ma.S¹
- ¹Chat
- ¹Pileolated Warbler, Ch², CF⁶, SaF⁴
- ¹Hooded Oriole, Sav²
- ¹Bullock Oriole, Sav², OW², Gr⁴
- ¹Brewer Blackbird, Sav², Gr², OW², CF⁴, MF⁴, Ma.F², SB², PJ²
- ¹Brown-headed Cowbird, Gr², SB², OW⁴, PJ²
- ¹Summer Tanager
- ¹Cardinal
- ¹Black-headed Grosbeak, OW², MF⁴, CF⁴, PJ²
- ¹Blue Grosbeak, Ma.F²
- ¹Lazuli Bunting, Ch², Gr²
- ¹Purple Finch, CF¹, MF³, OW²
- ¹House Finch, Sav², DS², Gr², OW⁴, G.JC², PJ¹, SB⁴, Ch⁶
- ¹American Goldfinch, Ch², Gr²
- ¹Arkansas Goldfinch, Sav², OW², Ch⁴, Gr², CF⁴, PJ¹, SB²
- ¹Spotted Towhee, Ch¹, SB², CF⁴, OW², PJ²
- ¹Brown Towhee, Ch¹, OW²
- ¹Abert Towhee, DS²
- ¹Fox Sparrow, Ch¹
- ¹Song Sparrow, Ma.F², Ch², Ma.S⁴

SAVANNA

Savanna is not itself a major plant formation; it is a mixture, and in terms of plant ecology it is a seral or transitional entity. Savanna is used here in cataloguing bird distribution because it was thought that it might reflect the importance to birds of mixture and of extensive "edge" conditions. Comparison of its avifauna with that of a true major plant formation should therefore be instructive in relating the biome concept to bird distribution in general. Some of the birds typical of savanna seem more responsive to the state of mixture than to any one of the separate elements that compose it.

The savanna as here defined is fundamentally a combination of very widely spaced trees with grassland (pl. 35a) or with grass and scattered brush. The trees, except where they form a small clump or short row, are not in contact and typically are 50 yards or more apart. Thus grassland exists with little influence from the trees. Savanna differs from piñon-juniper woodland in the dominance of grass rather than brush in the openings and in prevaillingly less rocky and precipitous ground surface; the sparser tree growth is perhaps a less important difference.

The savanna is unlike desert scrub in the presence of true trees, of less xerophilous aspect, and in substantial development of grass; in wide spacing of the larger plants the two are similar.

Savanna is thought to be a better term than parkland for the situation here described because the grass is dry during much of the year and the shrubs that do occur are xerophilous.

Savanna in California commonly involves valley, blue, and live oaks (*Quercus lobata*, *Q. douglasii*, *Q. agrifolia*), less often widely spaced conifers, especially junipers, the last usually being associated with extensive brush rather than grass. The formation may consist of farm plantings of occasional trees, which, unless they form a riparian belt, may provide a mixture with grassland or cultivated land that resembles original savanna. This type of artificial savanna has increased greatly in the lower valleys of California in the last fifty years. Thus originally pure grassland has taken on the qualities of savanna, and chaparral, desert scrub, and woodland have been cleared and opened up to accomplish a similar end. Some arroyos and washlands, too arid and too sparsely grown to broad-leaved trees to qualify as riparian tracts, may fall into the category of savanna.

Savannas occur chiefly west of the Cascade-Sierran axis at low levels, although locally they occur in the Great Basin and, through human agencies, in such areas as the Owens, Coachella, and Imperial valleys. Savanna is essentially absent from the northwestern coastal district.

Zonally, savanna lies primarily in the Upper Sonoran, but also it is extensive, under man's influence, in the Lower Sonoran.

The birds listed for savanna total 26, of which a large number, 16, or 61 per cent, show first preference for this situation. The total number of occupants is not great in view of our certainty of the general significance to birds of mixed situations. However, this number is probably not reliable, as incidental or secondary ecologic attachments have not been listed so liberally for savanna as for some of the true formations. Thus a species listed for oak woodland, although actually using savanna or one phase of it, might not have been listed because the peculiar mixed feature of savanna seemed to hold no attraction for the species; in short, there has been a bias against this exceptional sort of category for which it is not possible to compensate accurately. However, the 16 species listed as showing first preference are of significance. This total is equivalent to that for desert scrub and oak-woodland formations and is greater than those for sagebrush, grassland, and coastal forest.

It is further noteworthy that this mixed formation, although having a large number of species that show first preference, has no species with exclusive adherence. This results from its mixed aspect, which logically requires listing of grassland and woodland also if a species is primarily a savanna type, and from the close resemblance of piñon-juniper woodland to this mixture. Striking also is the large proportion of bird species of eurytopic character.

Affinity scores of the mixture are, as would be anticipated, chiefly with the separate elements that compose it, first with grassland, but in the aggregate even more with the three types of woodland—riparian, piñon-juniper, and oak (fig. 1).

BIRDS OF THE SAVANNA FORMATION

- 1Turkey Vulture, OW², Gr², Ch⁴, G.I.C², G.S.C², SB², RW², DS², PJ¹⁰, MF¹¹, CF¹¹, SaF¹¹
 2California Condor, G.I.C¹, Ch², Gr², MF⁴, OW², PJ⁷, SB⁸
 3White-tailed Kite, RW¹, Ma.F², Gr⁴, Ma.S²
 4Red-tailed Hawk, OW², Gr¹, G.I.C¹, RW², Ch⁴, MF⁷, PJ², SB², DS¹⁰, SaF¹¹
 5Swainson Hawk, Gr², PJ², SB⁴, DS⁵
 6Golden Eagle, OW², Gr², G.I.C⁴, MF⁵, SaF⁶, PJ¹, Ch², SB²
 7Sparrow Hawk, OW², Gr², RW⁴, PJ³, G.I.C², MF⁷, SaF⁸, DS⁹, SB¹⁰, CF¹¹
 8Mourning Dove, OW², RW², DS⁴, PJ², Gr²
 9Barn Owl, G.I.C¹, Gr¹, OW⁴
 10Horned Owl, OW¹, G.I.C¹, RW⁴, DS¹, MF², CF⁷, SaF⁸, PJ², Gr¹⁰, SB¹¹, Ch¹²
 11Eastern Kingbird, Gr¹, RW²
 12Western Kingbird, G¹, PJ²
 13Cassin Kingbird, PJ²
 14Purple Martin, CF¹, OW⁴, MF²
 15Yellow-billed Magpie, OW², Gr², RW⁴
 16Holarctic Raven, G.S.C¹, G.I.C¹, G¹, DS⁴, SB⁵, PJ², SaF⁵
 17American Crow, RW¹, OW², Gr⁴, CF², G.S.C²
 18Mockingbird, DS², PJ²
 19Mexican Bluebird, OW¹, MF², Gr⁴, RW², CF², PJ¹, SaF⁵
 20Loggerhead Shrike, G², PJ¹, DS⁴, SB², OW²
 21Hooded Oriole, RW¹
 22Bullock Oriole, RW¹, OW², Gr⁴
 23Brewer Blackbird, Gr², OW², CF⁴, MF², RW², Ma.F⁷, SB², PJ²
 24House Finch, DS¹, Gr², OW⁴, G.I.C², RW², PJ², SB², Ch²
 25Arkansas Goldfinch, OW², RW², Ch⁴, Gr², CF², PJ¹, SB²
 26Lark Sparrow, Gr², OW², Ch⁴, DS², SB²

(GRASSLAND

No attempt has been made to subdivide the grassland formation in the way that has been done in the interior and eastern parts of the continent. The highly modified character of our grasslands, resulting from human use, and lack of adequate knowledge of the species involved has led to this decision to treat grasslands as a unit. Therefore, any fairly continuous ground cover of essentially vertically stemmed, narrow-bladed plants is classed as grassland. The grass may form a sod or there may be bare ground about the bases of plants. To constitute the typical formation, large expanses of grass must be present (pl. 35b). However, one must recognize the coexistence in savanna (see p. 556) of patches of grass 50 yards or more across with the occasional trees of this formation.

The grasses may be of either annual or perennial type and may be mixed with low annual herbs. Sedges may be intermixed in damp meadows. Some situations included are open sparse grass on hard-packed, otherwise bare ground, short grasses dry and dead during most of the year, taller dense grasses up to 36 inches high (not commonly in California), mountain meadows, planted grain, and large tracts of lawn. Excluded are flooded meadows (which fall better with marshland), alpine turf, and narrow borders of grass about marshes and ponds or at edges of forests where the extent typical of grassland is not developed. Yet we recognize that some birds that use grass for foraging resort to these narrow belts as readily as they do to large expanses of true grassland.

Grassland is widespread in California, but predominates chiefly in the great valleys and foothills of the Pacific drainage and in the lake basins of the Modoc plateau. It is distinctly local in the northwestern coastal district and in the Sierra Nevada.

Zonal limitation is lacking. Grassland ranges from Lower Sonoran to Hudsonian. In the Alpine-Arctic it is replaced by alpine turf or meadow, which is perhaps merely a variety of grassland as far as birds are concerned.

The avifauna of grassland is rather large, consisting of 55 species. However, only 9, or 16 per cent, show exclusive or primary adherence to the formation. The number of true grassland species is smaller than the number (16) showing primary adherence to savanna. Extensive use of grass for forage ground without dependence on it for retreats or for nesting partly accounts for the large total avifauna. Also, inclusion of many varieties of grassland, great zonal range, and numerous contacts with other plant formations are contributory factors.

Affinities with other formations are very numerous (fig. 1). The highest relationship is with fresh-water marsh, mainly because of the use of both by many waterfowl, but also because of frequent proximity and resemblance in life-form of the plants involved in the two. Other scores are not individually significant, but reflect the great geographic and ecologic range of the formation.

BIRDS OF THE GRASSLAND FORMATION

- *Great Blue Heron, Ma.F¹, W.Fl.², W.Lac.³, Ma.S⁴, G.SS⁵, W.Lit.⁷
- *Canada Goose, Ma.F¹, W.Lac.³
- *Turkey Vulture, Sav⁴, OW⁵, Ch⁶, G.IO⁸, G.SC⁹, SB¹⁰, RW¹¹, PJ¹², MF¹³, CF¹⁴, Sa.F¹⁵
- *California Condor, G.IO⁸, Ch⁶, MF¹³, OW⁵, Sav⁴, PJ¹², SH¹⁶
- *White-tailed Kite, RW¹¹, Ma.F¹, Sav⁴, Ma.S⁴
- *Marsh Hawk, Ma.F¹, Ma.S⁴
- *Red-tailed Hawk, Sav⁴, OW⁵, G.IO⁸, RW¹¹, Ch⁶, MF¹³, PJ¹², SB¹⁰, DS¹⁰, Sa.F¹⁵
- *Swainson Hawk, Sav⁴, PJ¹², SB¹⁰, DS¹⁰
- *Golden Eagle, Sav⁴, OW⁵, G.IO⁸, MF¹³, Sa.F¹⁵, PJ¹², Ch⁶, SH¹⁶
- *Prairie Falcon, G.IO⁸, DS¹⁰, SB¹⁰
- *Sparrow Hawk, Sav⁴, OW⁵, RW¹¹, PJ¹², G.IO⁸, MF¹³, Sa.F¹⁵, DS¹⁰, SB¹⁰, CF¹⁴
- *Sharp-tailed Grouse
- *California Quail, Ch⁶
- *Sandhill Crane, Ma.F¹, W.Lac.³
- *Killdeer, W.Lac.³, W.Fl.², Ma.F¹, Ma.S⁴, G.SS⁵
- *Long-billed Curlew, Ma.F¹
- *Mourning Dove, Sav⁴, OW⁵, RW¹¹, DS¹⁰, PJ¹²
- *Barn Owl, G.IO⁸, Sav⁴, OW⁵
- *Horned Owl, OW⁵, Sav⁴, G.IO⁸, RW¹¹, DS¹⁰, MF¹³, CF¹⁴, Sa.F¹⁵, PJ¹², SB¹⁰, Ch⁶
- *Burrowing Owl, DS¹⁰
- *Short-eared Owl, Ma.F¹, Ma.S⁴
- *Trilling Nighthawk, DS¹⁰
- *Eastern Kingbird, Sav⁴, RW¹¹
- *Western Kingbird, Sav⁴, PJ¹²
- *Say Phoebe, G.IO⁸, DS¹⁰
- *Horned Lark, AM¹⁷
- *Bank Swallow, G.IO⁸, G.SC⁹
- *Rough-winged Swallow, G.IO⁸, G.SC⁹
- *Barn Swallow, G.IO⁸, G.SC⁹
- *Cliff Swallow, G.IO⁸

- *Yellow-billed Magpie, Sav¹, OW², RW⁴
 *Holarctic Raven, G.SC¹, G.IO², DS¹, SB², PJ², Sav¹, SaF²
 *American Crow, RW¹, OW¹, Sav², CF², G.SS²
 *Robin, MF¹, SaF², CF⁴, AM², RW²
 *Mexican Bluebird, OW¹, MF¹, Sav¹, RW², CF², PJ², SaF²
 *Loggerhead Shrike, Sav¹, PJ², DS¹, SB², OW²
 *Bobolink
 *Western Meadowlark
 *Red-winged Blackbird, Ma.F¹
 *Tricolored Blackbird, Ma.F¹
 *Bullock Oriole, RW¹, Sav², OW²
 *Brewer Blackbird, Sav¹, OW², CF⁴, MF², RW², Ma.F², SB¹, PJ²
 *Brown-headed Cowbird, RW¹, SB², OW⁴, PJ²
 *Lazuli Bunting, Ch¹, RW²
 *House Finch, Sav¹, DS¹, OW⁴, G.IO¹, RW², PJ¹, SB², Ch²
 *Pine Siskin, SaF¹, CF², MF², AM²
 *American Goldfinch, RW¹, Ch²
 *Arkansas Goldfinch, Sav¹, OW², RW², Ch⁴, CF², PJ², SB²
 *Lawrence Goldfinch, OW¹, MF², Ch⁴
 *Savannah Sparrow, Ma.F², Ma.S²
 *Grasshopper Sparrow
 *Lark Sparrow, Sav¹, OW², Ch⁴, DS², SB²
 *Rufous-crowned Sparrow, Ch¹
 *White-crowned Sparrow, Ch¹, AM²
 *Lincoln Sparrow

ALPINE MEADOW

Alpine meadows are, for the purposes of birds, essentially grassland with limited seasonal availability. Their special features are location at or above timberline, with the concomitants of climate, and the predominance of sedges in the complex (pl. 36a). Dwarf willows and small clumps of forbs are elements additional to the turf. Excluded are forest-enclosed meadows.

Zonally the meadows are Alpine-Arctic and marginally Hudsonian. Their total area is small and lies chiefly along the summits of the Sierra Nevada and in the Cascade Mountains; elsewhere the occurrence is much restricted, as in the Warner, White, and San Bernardino mountains, and the development there may be scarcely typical.

The avifauna of this formation totals only 8, none of which is an exclusive or principal inhabitant of it. This impoverished avifauna is a reflection both of the limited number of species of birds adapted to utilize the formation and its small disconnected development in the state. It is used chiefly as a combined facility by birds typical of alpine or subalpine zones. Most notable is the rosy finch, to which alpine cliffs are of first importance, and the subalpine race of white-crowned sparrow, which requires some bush cover together with grassland which may be of a type lower zonally than alpine turf. Affinity scores (fig. 2) are chiefly with coniferous forest, because of combined use of the adjoining subalpine forest formation, and with grassland and rock cliffs. The scores are of low significance, however, in view of the small number of species involved.

BIRDS OF THE ALPINE MEADOW FORMATION

- *Horned Lark, Gr¹
 *Clark Nutcracker, SaF¹, MF²

- *Robin, MF¹, Gr², SaF³, Cl⁴, RW⁵
 *Mountain Bluebird, SaF¹, SB², MF³
 *Rusty Finch, G.IC⁴
 *Pine Siskin, SaF¹, CF², MF³, Gr⁴
 *Oregon Junco, SaF¹, MF², CF³, OW⁵
 *White crowned Sparrow, Ch¹, Gr²

COASTAL FOREST

Coastal forest is one of three divisions of the coniferous forests of the state. It consists of species requiring relatively great moisture. Atmospheric humidity is high and fogs are frequent and dense. The forest is compact in the typical subdivisions of this formation (pl. 36b, c). Even so, there is heavy undergrowth apart from chaparral borders. In the more open facies of the coastal forest, the forest floor is well covered with brush and there are few grassy parkways.

The typical coastal forests, which are composed of plant types ranging south from areas of extensive development in Washington, British Columbia, and Alaska, consist of the following dominants: (1) tideland spruce (*Picea sitchensis*) and lowland fir (*Abies grandis*) on seaward slopes; (2) redwood (*Sequoia sempervirens*) in the belt of heavy fog; and (3) Douglas fir (*Pseudotsuga taxifolia*), intermixed with redwood, but farther inland in relatively pure stands. Tan oak (*Lithocarpus densiflora*), laurel (*Umbellularia californica*), madrone (*Arbutus menziesii*), and alders are commonly mixed with the conifers; other oaks in the areas of coastal forest tend to form distinct patches of oak woodland. Forest understory includes such shrubs as *Vaccinium*, *Gaultheria shallon*, *Acer circinatum*, *Rhus diversiloba*, *Ribes*, and *Rhododendron*. Chaparral developments of these shrubs in clearings and of these and plants of related growth form on unforested sea bluffs are not grouped with the forest formation, even though they may be serally related.

Appended to the true coastal forests are the Monterey forests, consisting of Monterey and Bishop pines (*Pinus radiata* and *Pinus muricata*), and very locally, originally, cypresses (*Cupressus macrocarpa*, *C. pygmaea*). This forest, of distinctly different floristic history, and associated with the central coastal fog belt, seems to be unaccounted for in Clements' groupings. In growth form it somewhat resembles montane forests of yellow pine, yet it is not so arid or so open as yellow pine forest, nor is its understory similar. In physical aspect it may be regarded as intermediate between montane and coastal forests, whereas in its contacts and in climatic conditions (prevalence of fog, especially in summer; lack of snow) it is most nearly related to the true coastal coniferous forests. For those last reasons, then, the Monterey forest association is included here.

Coastal forest extends southward from the Oregon line to San Luis Obispo County, in a narrowing belt. South of San Francisco Bay it is confined mainly to headlands, seaward slopes, and isolated humid pockets. Northward the interior limits are irregular, with interdigitations with, and inclusions of, montane forest and oak woodland. The inner limits run through interior Sonoma County, middle Mendocino County, and along the inner borders of Humboldt and Del Norte counties.

Zonally the formation is Transition. Parts of it northwardly have been classed as Canadian, but the grounds for this seem to me unsatisfactory; such classification

also does not conform to the zonal mapping for coastal areas of Oregon (Birds of Oregon, Gabrielson and Jewett, 1940).

Coastal forest has a total avifauna of 58 species, which is somewhat smaller than the avifaunas of montane forest and oak woodland. Possibly this lesser number is due to the compactness of the forest, but the avifauna in any event is large. The number of exclusive and principal adherents is 13, or 22 per cent, which is low. This results mainly from the fact that the three coniferous forests have a large avifauna in common, many species of which seem to develop greater population densities and occur over greater areas in the montane forest. Such species listed for the coastal forest are of second and third rating there as a consequence. There are, however, eight races of species with other principal affinities which as races are endemic to the coastal forest, a circumstance which adds to its distinctive qualities as a formation.

The fundamental affinity of the three coniferous forest formations is clearly shown in the relationship scores (fig. 1). Coastal forest shows dominant relation to montane forest with which it is zonally comparable; the strong affinity is caused in part by inclusion in coastal forest of an intermediate association, the Monterey forest. Subalpine forest is next in point of relationship, but it is scarcely higher in score than the two woodlands that have contact with coastal forest, namely, oak and riparian. Other affinities are few and weak.

BIRDS OF THE COASTAL FOREST FORMATION

¹Turkey Vulture, Sav¹, OW², Gr², Ch¹, G.I.C³, G.S.C³, SB², RW², DS², P.J.¹⁰, MF¹¹, Sa.F¹²

²Cooper Hawk, RW¹, OW², MF³, P.J.⁴

³Sharp-shinned Hawk, MF¹, OW²

⁴Sparrow Hawk, Sav¹, OW², Gr², RW⁴, P.J.⁵, G.I.C⁶, MF⁷, Sa.F⁸, DS⁹, SB¹⁰

⁵Sooty Grouse, MF¹, Sa.F²

⁶Mountain Quail, Ch¹, OW², MF³, P.J.⁴

⁷Band-tailed Pigeon, OW¹, MF²

⁸Screech Owl, OW¹, RW², DS³, P.J.⁴

⁹Horned Owl, OW², Sav³, G.I.C⁴, RW⁵, DS⁶, MF⁷, Sa.F⁸, P.J.⁹, Gr¹⁰, SB¹¹, Ch¹²

¹⁰Pigmy Owl, MF², OW³, P.J.⁴

¹¹Spotted Owl, MF², OW³

¹²Vaux Swift

¹³Allen Hummingbird, Ch¹

¹⁴Red-shafted Flicker, RW¹, MF², OW³, Sa.F⁴, P.J.⁵

¹⁵Pileated Woodpecker, Sa.F¹, MF²

¹⁶Acorn Woodpecker, OW¹, MF²

¹⁷Yellow-bellied Sapsucker, MF¹, RW², Sa.F³

¹⁸Hairy Woodpecker, MF¹, Sa.F², RW³, P.J.⁴

¹⁹Downy Woodpecker, RW¹, OW²

²⁰Western Flycatcher, RW¹, MF², OW³

²¹Western Wood Pewee, MF¹, Sa.F², OW³, RW⁴

²²Olive-sided Flycatcher, MF¹, Sa.F²

²³Violet-green Swallow, MF¹, G.I.C², OW³

²⁴Tree Swallow, RW¹, Ma.F², MF³

²⁵Purple Martin, OW¹, MF², Sav³

²⁶Canada Jay, Sa.F¹

²⁷Stellar Jay, MF¹, Sa.F², OW³, RW⁴

²⁸American Crow, RW¹, OW², Sav³, Gr⁴, G.S.S⁵

* A race occurs with primary affinity for coastal forest.

- ¹Chestnut-backed Chickadee, RW², OW²
- ²-Pigmy Nuthatch, MF¹
- ¹Brown Creeper, MF², SaF¹
- ¹House Wren, OW¹, RW², MF², SaF¹, Ch²
- ¹Winter Wren, MF²
- ¹Robin, MF¹, Gr¹, SaF², AM¹, RW²
- ¹Varied Thrush
- ²Hermit Thrush, SaF¹, MF²
- ¹Swainson Thrush, RW¹
- ²Mexican Bluebird, OW¹, MF¹, Sav¹, Gr¹, RW², PJ¹, SaF²
- ¹Golden crowned Kinglet, SaF², MF²
- ¹Cedar Waxwing
- ¹Hutton Vireo, OW¹, RW²
- ¹Orange crowned Warbler, Ch¹, OW², RW², SaF¹, MF²
- ²Audubon Warbler, SaF¹, MF¹
- ¹Black-throated Gray Warbler, OW¹, PJ¹, MF¹
- ¹Hermit Warbler, MF¹, SaF²
- ²Tolmie Warbler, Ch¹, RW², MF¹, SaF²
- ¹Pileolated Warbler, RW¹, Ch¹, SaF¹
- ¹Brewer Blackbird, Sav¹, Gr¹, OW², MF², RW², Ma.F², SB², PJ²
- ²Western Tanager, MF¹, SaF², OW¹, PJ¹
- ¹Black-headed Grosbeak, RW², OW², MF², PJ²
- ¹Evening Grosbeak, SaF¹, MF¹
- ¹Purple Finch, MF², OW², RW²
- ¹Pine Siskin, SaF¹, MF², Gr¹, AM²
- ¹Arkansas Goldfinch, Sav¹, OW², RW², Ch¹, Gr¹, PJ¹, SB²
- ²Red Crossbill, SaF¹, MF²
- ¹Spotted Towhee, Ch¹, RW², SB², OW², PJ²
- ¹Oregon Junco, SaF¹, MF², AM¹, OW²
- ¹Chipping Sparrow, MF¹, SaF², OW², PJ¹

MONTANE FOREST

This type of forest formation consists of relatively open stands of conifers, the forest floor of which is well exposed and dry in summer but is snow-covered during part of the winter (pl. 37a). There may be scattered bushes, or grasses and herbs in almost parklike arrangement. Trees of the forest are from 30 feet to more than 100 feet high. Dense tracts of bushes associated with this forest in developmental stages are, for our purposes, classed with the chaparral formation. Excluded also are tracts of black oaks (*Quercus kelloggii*) and golden oaks (*Quercus chrysolepis*), which are not intermixed with the conifers.

The principal forest dominants are *Pinus ponderosa*, *Libocedrus decurrens*, *Pinus jeffreyi*, *Pinus lambertiana*, and *Abies concolor*. The last and *Pseudotsuga taxifolia* and *P. macrocarpa* occur chiefly in shadier, cooler situations. Contrastingly, the above-mentioned oaks and *Quercus garryana* are intermixed in the more highly insolated facies of the forest; *Sequoia gigantea*, *Pinus coulteri*, *Pinus tuberculata*, and *Arbutus menziesii* locally or marginally contribute to the montane forest formation.

On the forest floor, beside sparse grass and forbs, green or dry according to season, are numerous kinds of shrubs of which the following genera are typical or exemplary: *Arctostaphylos*, *Ceanothus*, *Castanopsis*, *Symphoricarpos*, *Ribes*, *Rhus*, *Chamaebatia*.

* A race occurs with primary affinity for coastal forest.

The formation as here indicated coincides exactly with Clements' concept of it except for his inclusion of the chaparral subclimax. Zonally the formation is Transition and lower Canadian. The Jeffrey pine forest, which in openness of branchwork and stand is clearly like montane forests of lower levels, is the one truly Canadian Zone forest association that is grouped with this formation.

Geographically, montane forest extends throughout the lower middle levels of the Sierra Nevada-Cascade system, the Siskiyou and Trinity mountains west through Siskiyou and Trinity counties, and the inner northern Coast Ranges south to inner Lake County. Southward there are small developments in the inner central Coast Ranges and the Santa Barbara mountains, and there are larger areas on the high disjunct mountain groups of southern California. Eastward the forest occurs on high parts of the Modoc plateau, in the Warner Mountains, and very restrictedly east of Owens Valley in the Inyo district. The mapped outlines of the Transition Zone (Grinnell, 1935), exclusive of the areas already defined as coastal forest, represent at the lower margin the distribution of montane forest.

Montane forest supports a large avifauna, totaling 70 species. It is thus a richer avifauna than that of the other two coniferous forests. There are 22, or 31 per cent, that show principal affinity to this formation. Again, as in the coastal forest, the number is not great because many species are shared by the three forest formations. Proportionately it is intermediate between coastal and subalpine forest, although in actual numbers it is equal to the latter. In view of the uniformity of the formation florally, climatically, and zonally throughout its wide range, the size of the avifauna is surprisingly large. Probably an important favorable factor is the openness of the forest, which allows development and access to plants other than the dominant trees.

As would be expected, affinities of the formation with regard to birds are chiefly with the other two conifer formations in about equal degree (fig. 1). Oak woodland shows considerable affinity, partly because of intermixture and partly through similarities in form. Other formations are weakly related, although there is a wide range of minor affinities.

BIRDS OF THE MONTANE FOREST FORMATION

¹Buffle-head Duck, W.Lac.¹

²Turkey Vulture, Sav¹, OW², Gr², Ch¹, G.I.C², G.S.C², MH², RW², DN², P.J.², C.F.², Ss.F.²

³California Condor, G.I.C², Ch¹, Gr², OW², Sav¹, P.J.¹, MH²

⁴Goshawk, Sa.F.¹

⁵Cooper Hawk, RW², OW², P.J.¹, C.F.²

⁶Sharp-shinned Hawk, C.F.², OW²

⁷Red-tailed Hawk, Sav¹, OW², Gr², G.I.C², RW², Ch¹, P.J.², MH², DN², Ss.F.²

⁸Golden Eagle, Sav¹, OW², Gr², G.I.C², Sa.F.², P.J.¹, Ch¹, MH²

⁹Sparrow Hawk, Sav¹, OW², Gr², RW², P.J.², G.I.C², Sa.F.², DN², MH², C.F.²

¹⁰Sooty Grouse, Sa.F.², C.F.²

¹¹Mountain Quail, Ch¹, OW², C.F.², P.J.²

¹²Band-tailed Pigeon, OW², C.F.²

¹³Horned Owl, OW², Sav¹, G.I.C², RW², DS², C.F.², Sa.F.², P.J.², Gr², MH², Ch¹

¹⁴Flammulated Owl

¹⁵Pigmy Owl, C.F.², OW², P.J.²

¹⁶Spotted Owl, C.F.², OW²

¹ A race occurs with primary affinity for montane forest.

- ¹Saw-whet Owl, SaF¹, OW²
- ¹Booming Nighthawk, SaF¹
- ²Calliope Hummingbird, SaF¹
- ¹Red-shafted Flicker, RW¹, OW², CF³, SaF³, PJ²
- ¹Pileated Woodpecker, SaF¹, CF³
- ²Acorn Woodpecker, OW¹, CF³
- ¹Lewis Woodpecker, OW¹
- ¹Yellow-bellied Sapsucker, RW¹, SaF³, CF⁴
- ²Williamson Sapsucker, SaF¹
- ¹Hairy Woodpecker, SaF¹, CF³, RW², PJ²
- ¹White-headed Woodpecker, SaF¹
- ¹Wright Flycatcher, Ch¹, SaF¹
- ¹Western Flycatcher, CF¹, RW¹, OW⁴
- ¹Western Wood Pewee, SaF¹, OW¹, RW¹, CF³
- ¹Olive-sided Flycatcher, SaF¹, CF³
- ¹Violet-green Swallow, G.I.C², CF³, OW⁴
- ¹Tree Swallow, RW¹, Ma.F², CF³
- ¹Purple Martin, CF¹, OW¹, Sav⁴
- ¹Stellar Jay, CF³, SaF³, OW⁴, RW²
- ¹Clark Nutcracker, SaF¹, AM¹
- ¹Mountain Chickadee, SaF¹, PJ²
- ¹White-breasted Nuthatch, OW¹, SaF³, PJ⁴
- ¹Red-breasted Nuthatch, SaF¹
- ¹Pigmy Nuthatch, CF¹
- ²Brown Creeper, CF³, SaF³
- ¹House Wren, OW¹, RW², CF⁴, SaF³, Ch³
- ¹Winter Wren, CF¹
- ¹Robin, Gr⁴, SaF³, CF⁴, AM³, RW³
- ¹Hermit Thrush, SaF¹, (J)³
- ¹Mexican Bluebird, OW¹, Sav⁴, Gr⁴, RW², CF³, PJ¹, SaF³
- ¹Mountain Bluebird, SaF¹, AM³, SI³
- ¹Townsend Solitaire, SaF¹
- ¹Golden-crowned Kinglet, CF¹, SaF³
- ¹Ruby-crowned Kinglet, SaF¹
- ¹Solitary Vireo, OW³, RW³
- ¹Orange-crowned Warbler, Ch¹, OW², RW², CF⁴, SaF³
- ¹Nashville Warbler, OW², Ch³
- ¹Virginia Warbler
- ¹Audubon Warbler, SaF¹, CF³
- ¹Black-throated Gray Warbler, OW¹, PJ¹, CF³
- ¹Hermit Warbler, SaF³, CF³
- ¹Tolmie Warbler, Ch¹, RW², CF³, SaF³
- ¹Brewer Blackbird, Sav¹, Gr³, OW², CF⁴, RW⁴, Ma.F¹, SB¹, PJ¹
- ¹Western Tanager, SaF³, CF³, OW⁴, PJ³
- ¹Black-headed Grosbeak, RW¹, OW², CF⁴, PJ²
- ¹Evening Grosbeak, SaF¹, CF³
- ¹Purple Finch, CF¹, OW³, RW⁴
- ¹Cassin Finch, SaF¹
- ¹Pine Siskin, SaF¹, CF³, Gr⁴, AM³
- ¹Lawrence Goldfinch, OW¹, Gr⁴, Ch⁴
- ¹Red Crossbill, SaF¹, CF³
- ¹Oregon Junco, SaF¹, CF³, AM⁴, OW³
- ¹Gray-headed Junco
- ¹Chipping Sparrow, SaF³, OW², PJ⁴, CF³

* A race occurs with primary affinity for montane forest.

SUBALPINE FOREST

This formation has considerable variety in density and height of trees. It is a cool forest in summer, either because of altitude or shading of dense foliage masses or both. Only the red fir association attains great height. The forest floor has little plant cover and is heavily snow-blanketed through a large part of the year. Forest-enclosed meadows, seeps, streams, and lakes are frequent (pl. 37*b*).

Forest trees are chiefly lodgepole pine (*Pinus contorta*), red fir (*Abies magnifica*), silver pine (*Pinus monticola*), mountain hemlock (*Tsuga mertensiana*), limber pine (*Pinus flexilis*), white-barked pine (*Pinus albicaulis*), and foxtail pine (*Pinus balfouriana*). Aspens (*Populus tremuloides*), although they may in some situations represent seral stages, nonetheless constitute a significant forest element in some mountain ranges, particularly eastward. Some thickets of alders, elderberry, and low willows and aspens (if not well-developed riparian borders) are included in this formation. Excluded from the complex are the Jeffrey pine and white fir forests, with attendant chaparral, and the alpine meadows at or above timberline.

The concept of this formation agrees closely with that of Clements'. Zonally it is coextensive with the Hudsonian and Canadian zones except that it excludes the aforementioned Jeffrey pine—white fir—chaparral associations of the lower Canadian. Subdivision of the subalpine formation to be useful should probably be of several categories in agreement with the several kinds of forest dominants listed above.

Geographically the formation occurs in the Sierra Nevada-Cascade system, in the disjunct higher mountains southward to the San Jacinto Mountains, and in a few high parts of the Trinity and Siskiyou mountains west to South Fork Mountain and south to northern Lake County.

The avifauna of the subalpine forest totals 53; 21, or 40 per cent, are principal or exclusive adherents, the largest percentage for any of the forest formations of the state. (For further discussion see accounts of montane and coastal forests.) Affinity is predominantly with the related and only adjacent forest type, the montane formation (fig. 1). Coastal forest is next in relation, as would be expected from the common characters of coniferous forests, although there is essentially no contact of the two. Other relationships are weak. That for the adjoining alpine meadow type is low because of the very small total avifauna of the latter.

BIRDS OF THE SUBALPINE FOREST FORMATION

¹Barrow Golden-eye, W.Lac.¹

²Turkey Vulture, Sav¹, OW², Gr², Ch², G.I.O², G.S.O², SB², RW², DS², PJ², MF², CF²

³Goshawk, MF³

⁴Red-tailed Hawk, Sav¹, OW², Gr², G.I.O², RW², Ch², MF², PJ², SB², DS²

⁵Golden Eagle, Sav¹, OW², Gr², G.I.O², MF², PJ², Ch², SB²

⁶Sparrow Hawk, Sav¹, OW², Gr², RW², PJ², G.I.O², MF², DS², SB², CF²

⁷Sooty Grouse, MF², CF²

⁸Horned Owl, OW², Sav¹, G.I.O², RW², DS², MF², CF², PJ², Gr², SB², Ch²

⁹Great Gray Owl

¹⁰Screech Owl, MF², OW²

¹¹Screech Owl, MF²

- ¹Calliope Hummingbird, MF³
- ¹Red-shafted Flicker, RW¹, MF², OW³, CF¹, PJ³
- ¹Pileated Woodpecker, CH³, MF¹
- ^{2,3}Yellow-bellied Sapsucker, MF¹, RW², CF³
- ¹Williamson Sapsucker, MF²
- ²Hairy Woodpecker, MF¹, CF³, RW⁴, PJ³
- ¹White-headed Woodpecker, MF¹
- ¹Arctic Three-toed Woodpecker
- ¹Hammond Flycatcher
- ²Wright Flycatcher, CH¹, MF³
- ²Western Wood Pewee, MF¹, OW², RW⁴, CF³
- ¹Olive-sided Flycatcher, MF¹, CF³
- ^{2,3}Canada Jay, CF¹
- ¹Stellar Jay, MF¹, CF³, OW⁴, RW³
- ¹Holarctic Raven, G.S.C¹, G.I.C¹, Gr³, DS⁴, SB⁵, PJ³, Sav⁷
- ¹Clark Nutcracker, MF¹, AM³
- ¹Mountain Chickadee, MF¹, PJ³
- ¹White-breasted Nuthatch, MF¹, OW³, PJ⁴
- ¹Red-breasted Nuthatch, MF³
- ¹Brown Creeper, CF¹, MF³
- ¹House Wren, OW¹, RW², MF³, CF⁴, CH³
- ¹Robin, MF¹, Gr², CF⁴, AM³, RW³
- ¹Hermit Thrush, CF², MF³
- ¹Mexican Bluebird, OW¹, MF³, Sav², Gr⁴, RW², CF³, PJ⁷
- ¹Mountain Bluebird, AM³, SB², MF⁴
- ¹Townsend Solitaire, MF¹
- ¹Golden-crowned Kinglet, CF¹, MF³
- ¹Ruby-crowned Kinglet, MF³
- ¹Warbling Vireo, RW¹, OW³
- ¹Orange-crowned Warbler, CH¹, OW¹, RW³, CF⁴, MF³
- ¹Audubon Warbler, MF³, CF³
- ¹Hermit Warbler, MF¹, CF³
- ¹Tolmie Warbler, CH¹, RW³, CF³, MF⁴
- ¹Pileolated Warbler, RW¹, CH¹, CF³
- ¹Western Tanager, MF¹, CF³, OW⁴, PJ³
- ¹Evening Grosbeak, MF³, CF³
- ¹Cassin Finch, MF³
- ¹Pine Grosbeak
- ¹Pine Siskin, CF³, MF³, Gr⁴, AM³
- ¹Red Crossbill, MF³, CF³
- ¹Oregon Junco, MF³, CF³, AM⁴, OW³
- ¹Chipping Sparrow, MF¹, OW³, PJ⁴, CF³

INLAND CLIFFS

This and some other habitats to follow that are characterized most importantly by physical environment are of a rather different order than the preceding terrestrial communities characterized by types of vegetation. They tend to afford but one major facility for existence and not so often a complete domicile within which the bird may carry out all its activities.

The category of inland cliffs consists essentially of steep geologic exposures mostly free of plant growth (pl. 38a). These exposures may be only a few feet high. Included are rocky cliffs of all sorts, sand and earth banks, and scattered

* A race occurs with primary affinity for subalpine forest.

rock outcrops. Man-made substitutes include buildings, bridges, and well rigs. Only cliffs and rocks that occur on the immediate seacoast are excluded. Their proximity to ocean beaches and water and to prevailing fog seems to justify setting them off as a distinct category.

Zonally and geographically there is no limitation of occurrence. However, inland cliffs are more abundant in desert areas, mountains, and arid woodlands than in areas of heavy coniferous forest, particularly those of the coast.

For inland cliffs 24 species may be listed. A high proportion of these, 13, or 54 per cent, show primary affinity to them. This is true in large part because of the

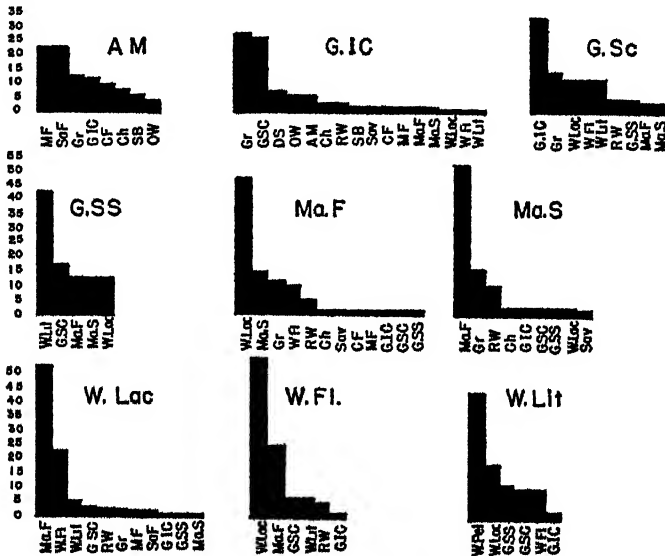


Fig. 2. Relationship scores for ecologic formations based on occurrences of birds (*continued*). For explanation see fig. 1.

nesting facilities afforded, and in a lesser degree because of roosting retreats. Few forage by preference in the habitat. One species, the white-throated swift, is listed here exclusively only because it seems to be indiscriminately aerial at all times except when at roost or nesting on cliffs. The condition is not greatly different in the swallows, although some conditions of terrestrial environment can be seen to influence their aerial forage beat; also some of them have additional nesting habitats.

Relationship with coastal cliffs is strong because of basic similarities in the two cliff habitats (fig. 2). Grassland shows high affinity because in open grassy terrain cliffs are commonly the sole shelter for birds; they substitute in a general way for tree growth. Otherwise relationships are of low value but of wide variety commensurate with the wide geographic and zonal range. Climate has only a weak, generalized influence on the occurrence of cliffs. The spread in relationships serves to emphasize how one facility for existence may control to the extent of causing a group of species to transgress boundaries of many life-zones and floral communities.

BIRDS OF INLAND CLIFFS

- *Turkey Vulture, Sav¹, OW², Gr¹, Ch⁴, G.SC⁵, SB⁷, RW⁸, DS⁹, PJ¹⁰, MF¹¹, CF¹², SaF¹³
- *California Condor, Ch⁴, Gr¹, MF¹¹, OW², Sav¹, PJ¹⁰
- *Duck Hawk, G.SC⁵, Ma.F⁴, Ma.S¹
- *Prairie Falcon, Gr¹, DS⁹, SB⁷
- *Sparrow Hawk, Sav¹, OW², Gr¹, RW⁸, PJ¹⁰, MF¹¹, SaF¹³, DS⁹, SB¹⁰, CF¹²
- *Golden Eagle, Sav¹, OW², Gr¹, MF¹¹, SaF¹³, PJ¹⁰, Ch⁴, SB⁷
- *Red-tailed Hawk, Sav¹, OW², Gr¹, RW⁸, Ch⁴, MF¹¹, PJ¹⁰, SB⁷, DS⁹, SaF¹³
- *Barn Owl, Gr¹, Sav¹, OW²
- *Horned Owl, OW², Sav¹, RW⁸, DS⁹, MF¹¹, CF¹², SaF¹³, PJ¹⁰, Gr¹, SB⁷, Ch⁴
- *Black Swift, G.SC⁵
- *White-throated Swift
- *Belted Kingfisher, W.Fl.¹, W.Loc.³, W.Lit.⁴, G.SC⁵
- *Black Phoebe, RW⁸, G.SC⁵
- *Say Phoebe, Gr¹, DS⁹
- *Violet-green Swallow, MF¹¹, CF¹², OW²
- *Bank Swallow, G.SC⁵, Gr¹
- *Rough-winged Swallow, G.SC⁵, Gr¹
- *Barn Swallow, G.SC⁵, Gr¹
- *Cliff Swallow, Gr¹
- *Holarctic Raven, G.SC⁵, Gr¹, DS⁹, SB⁷, PJ¹⁰, Sav¹, SaF¹³
- *Canyon Wren
- *Rock Wren
- *Rosy Finch, AM³
- *House Finch, Sav¹, DS⁹, Gr¹, OW², RW⁸, PJ¹⁰, SB⁷, Ch⁴

SEA CLIFFS

Sea cliffs include rock faces and dirt banks that front on the ocean or on salt-water bays (pl. 38b). Proximity to marine shoreline and waters is an essential feature of this habitat, which otherwise is primarily a nesting and roosting facility, as are inland cliffs. Unlike inland cliffs, these coastal exposures often provide essential forage lookouts above the strand line, and at their bases there is, in the rocky intertidal zone, a special type of forage terrain. Specifically included in this category are talus, rocky ledges at tide level, and offshore rocks—in short, the rocky intertidal zone of headlands and islets as well as cliffs themselves. Onshore winds are typical, with resulting updrafts of air over the cliff faces most of the time. Fog and mist are frequent.

For this ecologic situation only 13 species have been listed. The number would be much increased if wintering shorebirds were included. Also it would be greater if primarily aquatic species closely restricted to marine littoral and pelagic waters were included; most of these must resort to sea cliffs and rocks for breeding. Some landfall is inescapable for the existence of pelagic birds, just as air and water are for other species; so, with perhaps a measure of inconsistency, we have not listed their nest sites as evidence of special habitat preference. Of those that are listed, 5, or 38 per cent, show primary affinity for sea cliffs. The highest relationship score (fig. 2) is shown with inland cliffs, as might be expected, since the physical situation is similar. Other fairly strong affinities are shown with the forage habitats of the cliff dwellers, namely grassland and bodies of water. Relationships are not as diversified as for inland cliffs because of the restriction altitudinally and geographically to the coastline. The zonal occurrence accordingly is limited; the coast lies entirely within the Upper Sonoran and Transition zones.

BIRDS OF SEA CLIFFS

- *Turkey Vulture, Sav¹, OW², Gr³, Ch⁴, G.I.C⁵, SB⁶, RW⁷, DS⁸, PJ¹⁰, MP¹¹, CR¹², SaF¹³
 *Bald Eagle, W.Lac.¹, W.Fl.²
 *Osprey, W.Lac.¹, W.Lit.², W.Fl.⁴
 *Duck Hawk, Ma.F³, Ma.S⁵, G.I.C⁶
 *Black Oyster catcher
 *Western Gull, W.Lit.², G SS³
 *Black Swift, G.I.C⁵
 *Belted Kingfisher, W.Fl.¹, G.I.C², W.Lac.³, W.Lit.⁴
 *Black Phoebe, G.I.C⁵, RW⁷
 *Bank Swallow, G.I.C⁵, G¹
 *Rough-winged Swallow, G I.C⁵, Gr³
 *Barn Swallow, G I.C⁵, Gr³
 *Holarctic Raven, G.I.C⁵, Gr³, DS⁸, SB⁶, PJ¹, Sav⁷, SaF¹³

SEASHORE

This category includes sandy and gravelly marine beaches (pl. 38*b*) and essentially bare mud flats, either of bays or of estuaries. Important features for birds are openness and relative flatness of terrain with absence of crevices or vegetation for hiding places. Periodic flooding by tide or wave action occurs. Rocky beaches and reefs are grouped with sea cliffs and are excluded here. Seashore might be subdivided logically into mud flats and sandy and gravelly shores, but the number of bird species characteristic of each in the breeding season is so small that this is impractical.

Zonal and geographic occurrence are obviously limited, as are those of other coastal ecologic situations (see p. 569).

The number of birds occurring as summer residents in seashore habitat is 7, as small a group as that found in alpine meadows. Only 2 show primary preference for this formation. Doubtless the lack of nesting and refuge cover is an important cause (compare salt-water marsh). Certainly there is a wealth of food supply for birds, as proved by the extensive use of seashores during winter and migration periods by shorebirds and gulls.

Relationships are principally with adjoining formations such as littoral waters, sea cliffs, and salt marshes, particularly the first (fig. 2). The relation to lacustrine waters is not especially significant; it results mainly from the listing of the snowy plover for that formation as a second choice, since bare shores of inland playas, which it occasionally occupies, have rather arbitrarily been grouped with the lake waters themselves.

BIRDS OF SEASHORES

- *Snowy Plover, W.Lac.³
 *Killdeer, W.Lac.³, W.Fl.², Gr³, Ma.F⁴, Ma.S⁵
 *Western Gull, G.S.C¹, W.Lit.²
 *Least Tern, W.Lit.²
 *Great Blue Heron, Ma.F⁴, W.Fl.², W.Lac.³, Ma.S⁵, Gr³, W.Lit.⁴
 *Black-crowned Night Heron, W.Lac.³, Ma.F⁴, Ma.S⁵
 *American Crow, RW⁷, OW², Sav⁷, Gr³, CF⁸

FRESH-WATER MARSH

This type of community, serial from the successional standpoint between aquatic and terrestrial formations, is for birds an important mixture of conditions. The essential aspects for birds are presence of water, ~~or~~ mud with colonizing plant

cover (pl 39a) and rich food sources afforded by plant life, directly or indirectly. Areas of open water are usually no more than 20 feet across, but occasionally they range up to 50 feet.

Some situations which have been grouped in this category are masses of tules and cattails, sedge clumps except where widely spaced or where well intermixed with grasses or where growing on steep slopes, grasses the bases of which are flooded for several weeks in the nesting season, brackish water plant growth ranging nearly to a state of full marine salinity, sloughs and lake borders with dense floating vegetation, and densely grass-grown or sedge-grown borders of ponds and streams

Excluded are extensive mud flats, open shores of inland lakes, and the larger expanses of water of rivers and lakes.

Fresh-water marshes occur in all sections of the state, but of course are rare southeastwardly. They are developed most extensively in the lowlands or basins of the Great Valley and the Modoc plateau. Zonal occurrence is chiefly Lower and Upper Sonoran, with less representation in Transition and rare presence in Canadian.

The total avifauna of fresh-water marshes is large—indeed, the largest among those of the aquatic and partly aquatic communities. Of the total of 54, 34, or 63 per cent, show exclusive or primary adherence to this community. This is a greater proportion than for any other community except pelagic waters, and the situation there is anomalous and not strictly comparable.

Many species of essentially aquatic birds make use of both marsh and open water. Those that seem more critically tied to plant cover, not only in nesting but also for retreat from danger, are classed first for marsh and second for either lake or river waters. The latter two are perhaps so closely related as to merit combination. Were they joined, aquatic species would be seen to be more nearly equally divided, both in total numbers and in principal adherents, between marsh and open fresh-water situations than is evident from the present classification.

The relationship scores (fig. 2) closely link fresh-water marsh with the lacustrine community in accord with the foregoing considerations. Salt-water marsh shows a much lower relation, chiefly because its avifauna is small. This in itself indicates a fundamental difference. Grassland shows a fairly strong relationship, probably because of prevalent adjacency of the two and because of some similarities in vegetative form. Fluvial waters and riparian woodlands show significant relationships because they are adjacent.

BIRDS OF FRESH-WATER MARSHES

¹Eared Grebe, W.Lac.¹

¹Least Grebe, W.Lac.¹

¹Western Grebe, W.Lac.¹

¹Pied-billed Grebe, W.Lac.¹

¹Great Blue Heron, W.Fl.¹, W.Lac.¹, Ma.S.¹, G.SS.¹, Gr.¹, W.Lat.¹

¹Common Egret, W.Lac.¹, W.Fl.¹

¹Snowy Egret, W.Fl.¹

¹Black-crowned Night Heron, W.Lac.¹, Ma.S.¹, G.SS.¹

¹Least Bittern

¹American Bittern

- ¹White-faced Glossy Ibis, W.Lac.²
- ¹Canada Goose, W.Lac.², Gr²
- ¹Fulvous Tree duck, W.Lac.²
- ¹Mallard, W.Lac.², W.Fl.²
- ¹Cinnamon Teal, W.Fl.², W.Lac.²
- ¹Blue-winged Teal, W.Lac.², W.Fl.²
- ¹Pintail, W.Lac.²
- ¹Baldpate, W.Lac.²
- ¹Gadwall, W.Lac.², W.Fl.²
- ¹Shoveller, W.Lac.²
- ¹Canvas-back Duck, W.Lac.¹
- ¹Redhead Duck, W.Lac.²
- ¹Ruddy Duck, W.Lac.¹
- ¹White-tailed Kite, RW¹, Sav¹, Gr¹, Ma S²
- ¹Marsh Hawk, Ma.S², Gr²
- ¹Duck Hawk, G.SC¹, Ma.S², G.IC⁴
- ¹Sandhill Crane, W.Lac.², Gr²
- ¹*Clapper Rail, Ma.S¹
- ¹Virginia Rail, Ma.S¹
- ¹Sora Rail
- ¹Black Rail, Ma.S¹
- ¹Yellow Rail
- ¹Black Gallinule, W.Lac.²
- ¹American Coot, W.Lac.¹, W.Fl.²
- ¹Killdeer, W.Lac.², W.Fl.², Gr², Ma.S², G.SS²
- ¹Long-billed Curlew, Gr¹
- ¹Willet
- ¹Wilson Snipe
- ¹Black-necked Stilt, W.Lac.²
- ¹Avocet, W.Lac.²
- ¹Wilson Phalarope
- ¹Black Tern, W.Lac.²
- ¹Forster Tern, W.Lac.²
- ¹Short-eared Owl, Ma.S², Gr²
- ¹Tree Swallow, RW¹, CF², MF⁴
- ¹Long-billed Marsh Wren
- ¹Yellow-throat, RW², Ma.S²
- ¹Yellow-headed Blackbird, W.Lac.²
- ¹Red-winged Blackbird, Gr²
- ¹Tricolored Blackbird, Gr²
- ¹Brewer Blackbird, Sav¹, Gr², OW², CF², MF², RW², SB², PJ²
- ¹Blue Grosbeak, RW²
- ¹Savannah Sparrow, Gr¹, Ma.S²
- ¹Song Sparrow, RW¹, Ch², Ma.S²

SALT-WATER MARSH

This category involves tidal flats on which there is dense vegetative cover. The most important plant type is *Salicornia* (pl. 39b). *Grindelia* bushes and some grasses (*Spartina*) and sedges may form part of the cover. The vegetation is flooded periodically, at least basally, and beneath it and between tracts of it are tidal channels, 1 to 20 feet wide, the larger of which are free of plants. The plant growth ranges typically from 6 to 30 inches in height. Tules and cattails are excluded since

* A race occurs exclusively in inland marshes of the Colorado River system.

they do not tolerate fully saline waters and are best classed with the brackish and fresh-water marsh community.

Salt-water marshes are scattered along the coastline, about bays and at the mouths of larger rivers. They thus are restricted to the Upper Sonoran and Transition zones of the coast.

The small avifauna, totaling only 13, is probably a reflection of the uniformity of this formation and also the grouping of the intermediate brackish-water marshes with the fresh-water marshes. Only two species show principal affinity to this formation, but to these may be added two species with endemic salt-marsh races, the song sparrow and the savannah sparrow.

Relationship scores are chiefly with fresh-water marshes (fig. 2). Grassland, again, is fairly strongly connected because of adjacency and some similarity in growth form of plants. Surprisingly insignificant is the relation to adjoining marine littoral waters. In regard to breeding species, birds do not seem to make much common use of salt marsh, apart from bordering mud flats, and open water. The situation is thus very different from the high degree of joint occupancy of fresh-water marsh and lacustrine waters. About coastal bays, birds may be seen where water and marsh are much intermixed, but for summer residence they will be found to be essentially concerned with one or the other, seldom both.

BIRDS OF SALT-WATER MARSHES

¹Great Blue Heron, Ma.F¹, W.Fl.², W.Lac.³, G.SS⁴, Gr⁵, W.Lit.⁶

²Black-crowned Night Heron, W.Lac.¹, Ma.F², G.SS⁴

³White-tailed Kite, RW¹, Ma.F², Sav³, Gr⁴

⁴Marsh Hawk, Ma.F¹, Gr²

⁵Duck Hawk, G.SS¹, Ma.F², G.IC⁴

⁶Clapper Rail, Ma.F¹

⁷Virginia Rail, Ma.F¹

⁸Black Rail, Ma.F¹

⁹Killdeer, W.Lac.¹, W.Fl.², Gr³, Ma.F⁴, G.SS⁵

¹⁰Short-eared Owl, Ma.F¹, Gr²

¹¹Yellow-throat, Ma.F¹, RW²

¹²Savannah Sparrow, Gr¹, Ma.F²

¹³Song Sparrow, RW¹, Ma.F², Ch³

LACUSTRINE WATERS

No birds are completely aquatic, since their eggs must be tended out of water. Grebes, as well as a few other types, may, however, use vegetation that is free of the shoreline for nesting. In listing birds for aquatic formations it is understood that they have some nesting site on land or above the water. If the site does not closely limit the occurrence of the species in terms of other ecologic formations, it is disregarded in classifying the primarily aquatic species.

The lacustrine formation for birds consists essentially of bodies of water with the surface free of vegetation and of a depth of a foot or more (pl. 40a). There is no tidal action, but there may be seasonal fluctuation in level and wave action. Expanses of water 20 feet or more across, but usually 50 feet or more, have been considered lacustrine in contrast to small water surfaces included as parts of

* A race occurs that is restricted to salt-water marshes.

marsh formations. In these open areas there may be very sparse or scattered tules or patches of floating vegetation. Desert saline bodies are included, but not tidal salt or estuarine waters. The open margins of lakes are also included for lack of other useful treatment. Thus mud edges, border driftwood, and gravel and rock margins are grouped here, but not marshy or grassy vegetation.

Lacustrine waters occur widely in the state, apart from the coastline, although they are scarce on the desert. Zonally they are, of course, unlimited.

For this formation 47 species of birds are listed; 21, or 44 per cent, show principal or exclusive affinity. For discussion of the close relationships to marsh and fluviatile formations see pages 571 and 575, and figure 2. The relationship scores with other formations are low and of limited significance, except that their variety reflects the wide zonal and geographic occurrence of lacustrine bodies and the various contacts that lakes may have with other formations owing to absence of any close climatic control over their existence.

BIRDS OF LACUSTRINE WATERS

- ¹Common Loon
- ¹Eared Grebe, Ma.F²
- ¹Least Grebe, Ma.F²
- ¹Western Grebe, Ma.F²
- ¹Pied-billed Grebe, Ma.F²
- ¹White Pelican
- ²Double-crested Cormorant, W.Lit.¹, W.Fl.²
- ²Great Blue Heron, Ma.F¹, W.Fl.², Ma.S², G.SS², Gr², W.Lit.²
- ²Green Heron, W.Fl.¹, RW²
- ²Common Egret, Ma.F¹, W.Fl.²
- ¹Black-crowned Night Heron, Ma.F², Ma.S², G.SS²
- ²White-faced Glossy Ibis, Ma.F¹
- ²Canada Goose, Ma.F¹, Gr²
- ²Fulvous Tree-duck, Ma.F¹
- ²Mallard, Ma.F¹, W.Fl.²
- ²Cinnamon Teal, Ma.F¹, W.Fl.²
- ²Blue-winged Teal, Ma.F¹, W.Fl.¹
- ²Pintail, Ma.F¹
- ²Baldpate, Ma.F¹
- ²Gadwall, Ma.F¹, W.Fl.²
- ²Shoveller, Ma.F¹
- ²Wood Duck, W.Fl.¹, RW²
- ²Canvas-back Duck, Ma.F¹
- ²Redhead Duck, Ma.F²
- ²Barrow Golden-eye, Sa.F²
- ²Buffle-head Duck, MF²
- ²Ruddy Duck, Ma.F¹
- ²Common Merganser, W.Fl.²
- ²Bald Eagle, G.SS², W.Fl.²
- ²Osprey, W.Lit.², G.SS², W.Fl.²
- ²Sandhill Crane, Ma.F¹, Gr²
- ²Black Gallinule, Ma.F¹
- ²American Coot, Ma.F², W.Fl.²
- ²Killdeer, W.Fl.², Gr², Ma.F², Ma.S², G.SS²
- ²Spotted Sandpiper, W.Fl.¹
- ²Black-necked Stilt, Ma.F²
- ²Avocet, Ma.F¹

- ¹Ring-billed Gull
- ¹California Gull
- ¹Laughing Gull
- ²Black Tern, Ma.F¹
- ¹Gull-billed Tern
- ¹Caspian Tern, W.Lit.²
- ²Forster Tern, Ma.F¹
- ²Belted Kingfisher, W.Fl.¹, G.I.C.², W.Lit.⁴, G.S.C.¹
- ²American Dipper, W.Fl.¹
- ²Yellow-headed Blackbird, Ma.F¹

FLUVIATILE WATERS

For a general discussion of aquatic environments for birds see page 573. Fluviate bodies are nonsaline, moving masses of water with exposed surface. Rivers, streams, irrigation ditches, cascades, and parts of estuaries with tidal movements but without accompanying salinity are included. Usually the stream or stream channel is 20 feet or more across. Completely stagnant sloughs would fall with marsh or lacustrine formations, depending on size and condition of vegetation. Grouped with the fluviate waters are the barren margins of the stream course, with features such as gravel and mud bars, boulders, drift, and snags. Excluded are grassy margins, riparian growth, and cattails.

Geographic and zonal occurrence is broad, as with lacustrine waters. However, streams, in contradistinction to brooks or temporary outflows, are even scarcer on the desert than lacustrine bodies, and they are seldom developed above the Canadian Zone.

The fluviate community includes 19 species of birds. Most of these have more definite affinity with, or seem to be more successful in, lacustrine waters and fresh-water marshes; hence only 6, or 31 per cent, are rated with primary affinity for fluviate waters. The relationship scores are accordingly highest for these other fresh-water formations (fig. 2). Other relationships are few and are with riparian woodland, cliffs, and littoral waters. It is surprising that riparian woodland does not show a stronger relationship, but most aquatic species seem to be little dependent on the terrestrial formation beyond the immediate stream borders. The contrasts of environment are in general too great here for joint use or "edge" effect to become highly important.

BIRDS OF FLUVIATILE WATERS

- ¹Double-crested Cormorant, W.Lit.¹, W.Lac.²
- ²Great Blue Heron, Ma.F¹, W.Lac.², Ma.S⁴, G.S.S.², Gr.², W.Lit.⁷
- ¹Green Heron, W.Lac.², RW²
- ²Common Egret, Ma.F¹, W.Lac.²
- ²Snowy Egret, Ma.F¹
- ²Mallard, Ma.F¹, W.Lac.²
- ²Cinnamon Teal, Ma.F¹, W.Lac.²
- ²Blue-winged Teal, Ma.F¹, W.Lac.²
- ²Gadwall, Ma.F¹, W.Lac.²
- ¹Wood Duck, RW², W.Lac.²
- ¹Harlequin Duck
- ²Common Merganser, W.Lac.¹
- ²Bald Eagle, W.Lac.¹, G.S.C.²

⁴Osprey, W.Lac.¹, W.Lit.², G.SC³

⁵American Coot, W.Lac.¹, Ma.F²

⁶Killdeer, W.Lac.¹, Gr.², Ma.F³, Ma.S⁴, G.SS⁵

⁷Spotted Sandpiper, W.Lac.²

⁸Belted Kingfisher, G.IO², W.Lac.³, W.Lit.⁴, G.SC⁵

⁹American Dipper, W.Lac.²

MARINE LITTORAL WATERS

The marine littoral environment (pl. 40*b*) consists of saline and brackish waters within approximately two miles of shore and within bays and estuaries. Depth of water is not a serious factor for birds, since chiefly they work at or within a few feet of the surface. For discussion of the essential use of shore facilities see page 573. Wave action is typical of these waters, although it is absent in some bays. Tidal movements are of little consequence except as currents and variations in depth in bays are involved. The shore effect of tides is beyond the scope of this formation. Littoral species of birds, beside relying on food sources typical of these active and fairly shallow waters, are less able to cruise long distances from landfalls, particularly for roosting, than are truly pelagic species.

For littoral waters 16 species are listed; 5, or 31 per cent, show primary affinity for this situation. The relationship score (fig. 2) is high for pelagic waters, which of course adjoin and merge indefinitely with littoral waters. The score for lacustrine waters is fairly strong, with a lower score for fluviatile waters. Other relations are with cliffs and strand-line environments.

BIRDS OF MARINE LITTORAL WATERS

¹Double-crested Cormorant, W.Lac.², W.Fl.³

²Brandt Cormorant

³Pelagic Cormorant

⁴Brown Pelican

⁵Great Blue Heron, Ma.F¹, W.Fl.², W.Lac.³, Ma.S⁴, G.SS⁵, Gr.⁶

⁶Osprey, W.Lac.¹, G.SC², W.Fl.³

⁷Western Gull, G.SC¹, G.SS²

⁸Caspian Tern, W.Lac.²

⁹Least Tern, G.SS¹

¹⁰Common Murre, W.Pel.¹

¹¹Pigeon Guillemot, W.Pel.²

¹²Xantus Murrelet, W.Pel.¹

¹³Cassin Auklet, W.Pel.¹

¹⁴Rhinoceros Auklet, W.Pel.¹

¹⁵Tufted Puffin, W.Pel.¹

¹⁶Belted Kingfisher, W.Fl.¹, G.IO², W.Lac.³, G.SC⁴

PELAGIC WATERS

The important aspect of these waters for birds is their remoteness from landfalls. Essential use of land for nesting is assumed (see p. 573; pl. 40*b*), but water two or more miles offshore, frequented without daily recourse to land, is considered a pelagic situation for birds. The depth of the water is immaterial since it is all much deeper than necessary for diving operations, and tidal effects are not felt. Depth may, however, have indirect control on some food resources, nutrients in general being less than in littoral waters. Wave action is seldom absent.

Listed are 10 species, of which 9 are primarily of pelagic affinity. Relationships are exclusively with littoral waters, as might be expected in this terminal member of the series of formations for birds.

BIRDS OF PELAGIC WATERS

- ¹Fork-tailed Petrel
- ¹Leach Petrel
- ¹Ashy Petrel
- ¹Black Petrel
- ¹Common Murre, W.Lit.²
- ¹Pigeon Guillemot, W.Lit.¹
- ¹Xantus Murrelet, W.Lit.²
- ¹Cassin Auklet, W.Lit.²
- ¹Rhinoceros Auklet, W.Lit.²
- ¹Tufted Puffin, W.Lit.²

REVIEW

Of the total of 274 species tabulated according to ecologic formations, the greatest numbers occur in riparian woodland (75) and montane forest (70), with oak woodland, coastal forest, grassland, fresh-water marsh, and subalpine forest following in order (see table 3), and the others ranging down in numbers of species to seashore (7).

TABLE 3
SUMMARY OF OCCURRENCE OF AVIAN SPECIES IN ECOLOGIC FORMATIONS

Total species in each formation		Total species occurring exclusively in, or showing first preference for, each formation	
RW.....	75	Ma.F.....	34
MF.....	70	RW.....	33
OW.....	63	MF.....	22
CF.....	58	SaF.....	21
Gr.....	55	W.Lac.....	21
Ma.F.....	54	Ch.....	20
SaF.....	53	Ds.....	17
W.Lac.....	47	Sav.....	16
PJ.....	45	OW.....	15
Ch.....	43	CF.....	13
DS.....	40	G.IC.....	13
SB.....	20	W.Pel.....	9
Sav.....	26	Gr.....	9
G.IC.....	24	SB.....	7
W.Fl.....	19	W.Fl.....	6
W.Lit.....	16	G.Sc.....	5
G.Sc.....	13	W.Lit.....	5
Ma.S.....	13	PJ.....	4
W.Pel.....	10	G.SS.....	2
AM.....	8	Ma.S.....	2
G.SS.....	7	AM.....	0

A somewhat more significant picture may be derived by comparing numbers of species that occur exclusively in a given formation or show primary attachment to it. The same formations, on the whole, head the list. Of the 11 with the highest count in the first listing by total number, 9 appear among the first 11 in the second list, grassland and pifion-juniper dropping low with small numbers of prime adherents. Fresh-water marsh and chaparral have moved notably higher within the first 11 in the second type of ranking, and oak woodland and coastal forest have descended.

Table 4 shows that most species range through or utilize more than one formation. The greatest number ranges through two units; smaller percentages occur in

but one formation and in three formations, respectively. The situation is not unlike that with respect to zonal range, although there is a slightly higher percentage of single-formation species and a lower percentage of triple formation species. It should be pointed out, however, that the zonal system presents a series of six possible categories, whereas in the formational system seventeen units are available to approximately the same group of nonmarine species. Accordingly, on a mathematical basis alone, it would seem much more possible for a species to occur in several formations than in several zones. The formational or biome system, with its subdivisions as here employed, is therefore, a more exact means of cataloguing distributional information than is the zonal system.

TABLE 1
TOTAL RANGE OF FORMATIONS INHABITED BY BREEDING BIRDS

Range	Number of species	Percentage
1	67	24
2	57	32
3	54	21
4	23	8
5	17	6
6	10	4
7	2	
8	3	1
9	3	1
10	0	
11	2	
12	1	
13	1	
	271	

The affinities of different formations to one another, as reflected by relationship scores (figs. 1 and 2), have been indicated for each individual formation. Some general aspects of these relations we find to be the following. The highest absolute score, 11.89 (table 5), relating two ecologic situations is that for fresh-water marsh and lacustrine waters, a reflection of the usual mixture of these two in a small area and the prevalent use of, and need for, both by a large group of water birds. Otherwise the high scores (10-11) are those interrelating the three types of coniferous forest. This circumstance emphasizes the coniferous forest group or biome as a unit and suggests that the three subdivisions here used are less fundamental than some of the other subdivisions in the system. Distinctly lower scores are found between members of the woodland group; in fact, members of this group show as high scores for relation with coniferous forests as with other woodlands. In this same range of relationship values we find other intragroup ties, as between lacustrine and fluviatile waters (5) and between fresh- and salt-water marshes (4). Scores are low among members of the scrub group, the members tying as strongly to woodland formations as to other scrub types, with scores of about 3. A similar situation holds for the grassland group.

It is evident from table 6 that some of the terrestrial formations have no significant zonal restriction, as, for example, grassland; or that they have very little, as sagebrush, chaparral, and riparian woodland. However, such formations may not be equally prevalent throughout their zonal range. On the contrary, some formations, such as desert scrub and coastal forest, are of narrow zonal range.

One might reverse the comparison of zones and formations, in which event large formational groupings for terrestrial situations should be used. By so doing it is seen that the Alpine-Arctic Zone has a narrow range, associated only with the grassland (alpine meadow) formation, and that the Canadian Zone is associated only with the coniferous forest formation, whereas Upper Sonoran relates to many biomes. It is important to remember that the units of narrower range, whichever way the comparisons be made, do not necessarily remain narrow or identically restricted when traced over continental areas.

The lack of any strong concordance of zonal and formational units and the different climatic bases (temperature versus all aspects of climate) which underlie their development are sufficient reasons for regarding as unsound efforts to subordinate one system to the other. They are related systems, but are not phylogenetically derived one from the other; each has its own attributes and its own inadequacies as a master system.

Species which have a narrow zonal or a narrow formational range in the lists here presented have been compared to determine the degree of correspondence in limitation. A total of 180 species which had been rated as to both zone and formation showed limitation to one or two units in at least one of the systems. Of these, 124 that occur in no more than two zones occur in no more than three formations. Conversely, 99 that occur in no more than two formations occur in no more than two zones. There is, in other words, a combined group, out of the 180, of only 56 that show a distinctly broader range in one system than in the other. These 56 are particularly instructive in that one system but not the other affords the most satisfactory method of expressing the broad aspects of their distribution. Sixteen species of a zonal range of two occur in four or more formations. Some examples are California condor (8 formations), white-tailed kite (5), ash-throated flycatcher (5), violet-green swallow (5), loggerhead shrike (6), black-throated gray warbler (4), and Tolmie warbler (5).

Forty species of a formational range of two occur in three or more zones. However, 15 of these are marsh or stream dwellers which show a narrow formational range because of the exacting requirement of water surface and the small number of subdivisions which we have adopted for the aquatic or marsh environments. The 25 terrestrial species limited to one or two formations but with broader zonal range are more nearly equivalent to the opposite group of narrow zonal but broad formational range. Examples from among this 25 for which the formational range is the more restrictive are burrowing owl (3 zones), Traill flycatcher (4), horned lark (6), cliff swallow (4), rock wren (5), canyon wren (3), sage thrasher (4), yellow warbler (3), chat (3), western meadowlark (3), vesper sparrow (3), and Brewer sparrow (5).

In the species in which zonal and formational limitation are not equivalently restrictive it is important to realize that the less restrictive system nonetheless

often expresses some aspects of range limitation additional to the other system. For example, the black-throated gray warbler occurs only in the Upper Sonoran and Transition zones, but in coastal forest, montane forest, oak woodland, and piñon-juniper woodland. Diverse as may be the type of plant cover utilized, it still expresses a type of limitation additional to zone. There are thus other formations that range through Upper Sonoran and Transition that this warbler does not occupy, as, for example, chaparral and riparian woodland. An opposite situation is found in the chat, which occurs only in riparian woodland, but ranges from Lower Sonoran through Upper Sonoran into the lower parts of the Transition Zone. The zonal range is nonetheless partly restrictive, for the chat does not follow riparian woodland through the Transition and into the Canadian Zone.

Even among the species of restrictive distribution in both systems it should be realized that the two sets of restrictions usually supplement each other, expressing slightly or distinctly different facets of distributional control. For example, the Nuttall woodpecker occurs in the Lower and Upper Sonoran zones, chiefly the latter, and in oak woodland and to some extent riparian woodland. It does not occur in these woodlands in the Transition Zone and it does not occur in the Upper Sonoran Zone in the piñon-juniper and chaparral formations. Further, the verdin occurs only in the Lower Sonoran Zone and the desert scrub formation, not in riparian woodland or grassland of the Lower Sonoran. The Bell vireo occurs only in riparian woodland and the Lower Sonoran Zone, but not in the Upper Sonoran (except possibly marginally) or the Transition zones where riparian woodland occurs.

The general conclusion to be drawn is that zonal and formational systems are partly independent, each expressing a set of distributional facts, one often supplementing the other. For one group of species one appears more adequate than the other and for another group the opposite is true. More precision in general is registered by the formational system, partly because it is more finely divided, as here employed, and partly because it reflects climatic factors in addition to temperature; but its greater utility is not universally true. If, as contended, each system has its values and its set of factors to register or emphasize and the two are in a measure supplementary, there is little point in debating which is superior. The important thing is to know the values of each and to avoid improperly magnifying them.

FAUNAL GROUPS

Biotic provinces or areas are units that are primarily geographic, each of which may therefore contain several zonal strata and several biomes. Their only essential features seem to be some measure of distinctness of their faunas. Barriers, whether zonal, biotic, or physiographic, are the critical agents that set off an area and its fauna and keep it partly different from that of an adjoining area.

The customary descriptions of biotic units are subjective, with no well-formed criteria specified, and different authors evidently have different kinds of units in mind. A brief critique of the concept of the biotic province along these lines was presented earlier (Johnson, Bryant, and Miller, 1948:236-237). It was concluded that "a biotic area has significance . . . only as its fauna contains unique

forms and as its limits are set by the approximate coincidence of range boundaries of the unique forms and of parts of the boundaries of other members of its fauna. In continental areas boundaries will be sharp largely in conformance with the distinctness of boundaries of plant formations." How many ranges must coincide and how many forms must be different (differentiated, or present and absent) in adjoining areas to justify designation of the areas as distinct is an arbitrary matter, and a graded set of differences actually occurs.

It was also pointed out by us (*ibid.*:237) that in a system of biotic provinces too much emphasis is often placed on purely geographic aspects. It is best to stress actual faunas and their differences as much as or more than the areas and boundaries within which they occur, since faunas are "associations of species with similar, though not identical, climatic and biotic tolerances, with ranges partly in common, and often with similar areas of origin as species." Yet, admittedly, to define faunas may be just as difficult as to define biotic provinces.

The analysis which follows, then, is based, in the first place, on four major avifaunas, delimited admittedly somewhat arbitrarily, on the basis of strong or repeated association of species which have similar centers of distribution and probably often similar areas of origin. Three of these faunas may be thought of as intrusive with respect to California in that they center in areas beyond the state and range into it. These three are the Boreal, the Great Basin, and the Sonoran. The fourth avifauna is essentially endemic to the state and may be termed Californian. Each species and race is placed in one of the faunas or in a fifth group consisting of forms of extensive western North American occurrence and of those unclassifiable on any adequate grounds in the four principal faunas. Since this approach separates species partly in concordance with zonal and biomal limits, it relieves the faunal or biotic districts of some of the undesirable diversity of zonal and formational types which often have characterized biotic areas as marked out by other authors.

Within each of the four faunal groups the subfaunas occupy different areas within the state. These areas or provinces and their faunas are recognized and evaluated with fair objectivity by determining the actual degree of difference in make-up between them. This is done by matching lists of members of the fauna from two areas. A count of 1 is registered for each difference in the lists, that is, for each species or race in either area which is absent in the other; an exception is made for complementary races of the same species, whereby a count of 1 (not 2) is allowed for each pair of races. The total count is an index of difference reflecting, first, the forms that reach their limits of occurrence at the boundary between the areas, and second, forms that have differentiated within the areas and are endemic to them, and hence the "power" of the areas as differentiation centers.

BOREAL AVIFAUNA

The boreal avifauna pertains to the coniferous forest areas of the state. The area it occupies encompasses all developments of the coastal forest, montane forest, and subalpine forest formations. Some other formations are involved in minor degree: parts of the sagebrush, chaparral, riparian woodland, oak woodland, and grassland formations, all the alpine meadow formation, and some parts of the aquatic and

rockland communities. Because the lower and southern limits of the dominating coniferous forests—the boreal environment—serve in the main as boundary marks for the lower edge of the Transition Life-zone in California, the area occupied by the fauna can also be described with facility by zonal terms. The zones involved are the Transition and Boreal (= Canadian, Hudsonian, and Alpine-Arctic).

The boreal avifauna consists of (1) species of northern derivation, or at least those currently showing northern distribution centers, which range into the Californian extension of the boreal environment; (2) geographic races of boreal or nonboreal species which as races have differentiated in the boreal environments north or east of the state but which extend into it; and (3) races of boreal or fundamentally nonboreal species which have differentiated within Californian subdivisions or isolated tracts of the general boreal area.

The total number of boreal species listed (table 7) for the breeding season in California is 67. (A few additional species are entered in the table for purposes of comparing the Oregon fauna.) The total of boreal species and widespread boreal races of other species is 75 for California. In all, 132 forms (species and subspecies) fall within the foregoing definition of the boreal fauna.

The subfaunas of sixteen geographic areas have been listed and compared. Two of the areas, the Oregon coast and the Sierra San Pedro Mártir of Baja California, lie entirely outside California but are so intimately related to the problem of determining the faunal areas within the state that they must be considered in detail. Every well-detached area of boreal environment in California has been examined to see if it might merit separate treatment; this preliminary scrutiny led to the selection of the fourteen divisions of the state mapped in figure 3. Thus, breaks in continuity of forests, as that between the Marin peninsula and Sonoma County, or that between the San Bernardino and San Jacinto mountains, were followed in searching for natural groupings. Some of those finally selected proved to be of no great significance as faunal units, but, on the other hand, I think that no areas of major distributional significance have been passed over by this process. Also, some areas were recognized as distinct even though they were in full continuity with other boreal areas because it could be seen, by trial surveys of range outlines, that a considerable change in fauna took place at a fairly well-marked, narrow zone in a forest continuum.

The inclusive outlines for the boreal area (fig. 3) follow the borders of the coniferous forests and are drawn chiefly from life-zone maps since, as explained on page 586, the lower boundary of the Transition Zone coincides with the coniferous forest edge over much of the state. Small inclusions of nonboreal environments within the boreal area are not shown, nor are very small detached boreal areas. The boundaries between the subunits are readily determined when there are discontinuities in the forest, but elsewhere the boundaries represent compromises. For example, the boundary between the Humboldt and Sonoma areas represents approximately a midpoint for the actual range limits of 20 forms which occur within a span of 120 miles along the coastal strip. Six of these individual boundaries are in the vicinity of Albion and Fort Bragg, Mendocino County, five are about 35 miles farther north in the vicinity of latitude 40°, and eight are in the area just south of Humboldt Bay. However, the last group includes a number of species the precise breeding limits of which have not been well explored, and many

TABLE 7
THE BOREAL AVIFAUNA OF CALIFORNIA

	Oregon coast	Humboldt	Sonoma	Marin	Santa Cruz	Monterey	Trinity	Casas le	Warner	Sierra Nevada	Mount Pitts	San Bernardino	San Jacinto	San Diego mountains	Sierra San Pedro Martir	Inyo mountains
1. <i>Gavia immer</i>								x								
2. <i>Branta canadensis mollis</i>								x								
3. <i>Anas carolinensis</i>								x	x	x						
4. <i>Mareca americana</i>								x	x							
5. <i>Aythya valisineria</i>								x	x							
6. <i>Bucephala islandica</i>								x		x						
7. <i>Bucephala albeola</i>								x								
8. <i>Histrionicus histrionicus pacificus</i>										x						
9. <i>Mergus merganser americanus</i>	x	x				x	x	x		x						
[<i>Lophodytes cucullatus</i>].....	x															
10. <i>Accipiter gentilis atricapillus</i>							x	x	x	x						
a. <i>Accipiter striatus velox</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
<i>Dendragapus fuliginosus</i>																
<i>fuliginosus</i>	x	x	x													
11. <i>Dendragapus fuliginosus sierrae</i> ..							x	x	x	(x)						
<i>Dendragapus fuliginosus howardi</i>										x	(x)					x
12. <i>Bonasa umbellus sabini</i>	(x)	x					x									
<i>Oreortyx picta pulmeri</i>	(x)	x	x			x										
13. <i>Oreortyx picta picta</i>							x	x	x	(x)						
<i>Oreortyx picta crumiphila</i>										x	x	(x)	x	x	(n)	x
<i>Lophortyx californica brun-</i>																
<i>nescens</i>		(x)	x	x	x											
14. <i>Capella delicata</i>								x	x	x	x	x				
15. <i>Otus flammeolus</i>							x	x		x	x	x				x
<i>Otus asio brewsteri</i>	(x)	x														
<i>Bubo virginianus saturatus</i>	x	x	x	x	x											
16. <i>Glaucidium gnoma pinicola</i>																x
<i>Glaucidium gnoma californicum</i> ..							x	x		x	x	x	x	x		
<i>Glaucidium gnoma grinnelli</i>	x	x	x	x	x	x										
17. <i>Strix occidentalis caurina</i>	(x)	x	x	x			x									
<i>Strix occidentalis occidentalis</i>										(x)	x	x	x	x		
18. <i>Strix nebulosa nebulosa</i>										x						
b. <i>Asio flammeus flammeus</i>	x	x	x	x	x			x	x							
19. <i>Aegolius acadicus acadicus</i>	x	x	x	x	x		x	x	x	x	x	x	x	x		x
<i>Chordeiles minor hesperis</i>	x	x					x	x	x	x		x				
<i>Chaetura vauxi vauxi</i>	x	x	x	x	x											
<i>Selasphorus platycercus platy-</i>																
<i>cercus</i>																x
[<i>Selasphorus rufus</i>].....	x															
20. <i>Stellula calliope</i>							x	x	x	x	x	x	x		x	
<i>Colaptes cafer cafer</i>	x	x														
c. <i>Dryocopus pileatus picinus</i>	x	x	x	x			x	x		x						

Numbers at left of names mark boreal species.

Letters at left mark widespread boreal races.

Brackets indicate a species breeding outside California.

(x) denotes center of differentiation.

n denotes presence of another race, replacing the one named.

TABLE 7—Continued

	Oregon coast	Humboldt	Sonoma	Marin	Santa Cruz	Monterey	Trinity	Cascade	Warner	Sierra Nevada	Mount Pinos	San Bernardino	San Jacinto	San Diegoan mountains	Sierra San Pedro Mártir	Inyo mountains
21. <i>Asyndesmus lewis</i>							x	x	x	x	x					
22. { <i>Sphyrapicus varius nuchalis</i>																
<i>Sphyrapicus varius daggetti</i>	x	x					x	x		(x)	x					
23. <i>Sphyrapicus thyroideus thyroideus</i>							x	x	x	(x)	x	x	x			
<i>Dendrocopos villosus orius</i>							(x)	x	x	x						
<i>Dendrocopos villosus harrisi</i>	(x)	x														
<i>Dendrocopos villosus hyloscopus</i> ..			x	x	x	(x)	x			x	x	x	x	x	x	
<i>Dendrocopos villosus leuco-</i>																
<i>thorectis</i>																x
<i>Dendrocopos pubescens leucurus</i> ..																x
<i>Dendrocopos pubescens gairdnerii</i> ..	(x)	x														
{ <i>Dendrocopos albolarvatus albo-</i>																
<i>larvatus</i>							x	x	x	(x)	x					
24. <i>Dendrocopos albolarvatus</i>																
<i>gravirostris</i>												(x)	x	x		
25. <i>Picoides arcticus</i>								x	x	x						
26. <i>Empidonax hammondi</i>							x	x		x						
27. <i>Empidonax wrightii</i>							x	x	x	x	x	x	x			x
d. <i>Empidonax difficilis difficilis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
e. <i>Contopus richardsonii richardsonii</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
28. <i>Nuttallornis borealis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Eremophila alpestris sierrae</i>								x		(x)						
f. <i>Tachycineta thalassina lepida</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
29. { <i>Perisoreus canadensis griseus</i>							x	x	x							
<i>Perisoreus canadensis obscurus</i> ..	(x)	x														
30. { <i>Cyanocitta stelleri frontalis</i>	(x)	x	x				x	x	x	(x)	x	x	x	x		x
<i>Cyanocitta stelleri carbonaceu</i>				x	(x)	x										
<i>Aphelocoma coerulescens caurina</i> ..		(x)	x													
31. <i>Nucifraga columbiana</i>							x	x	x	x	x	x	x		x	x
32. <i>Parus atricapillus occidentalis</i>	(x)	x					x									
<i>Parus gambeli abbreviatus</i>							x	x	x	(x)						
33. { <i>Parus gambeli inyoensis</i>																(x)
<i>Parus gambeli baileyae</i>						x					x	(x)	x	x	(x)	
<i>Parus rufescens rufescens</i>	x	x	x				x									
34. { <i>Parus rufescens neglectus</i>				(x)												
<i>Parus rufescens barlowi</i>					(x)	x										
<i>Sitta carolinensis tenuissima</i>								x	x	x					(x)	(x)
35. <i>Sitta canadensis</i>	x	x	x	x			x	x	x	x	x	x	x			
<i>Sitta pygmaea melanotis</i>							x	x	x	x	x					
36. { <i>Sitta pygmaea pygmaea</i>			x	x	x	(x)										
<i>Sitta pygmaea leucocnucha</i>													x	x	(x)	
37. { <i>Certhia familiaris zelotes</i>							x	x	x	(x)	x	x	x	x		x
<i>Certhia familiaris occidentalis</i> ..	x	x	x	x	x	x										
<i>Chamaea fasciata rufula</i>	(x)	x	(x)	x												
<i>Chamaea fasciata fasciata</i>					(x)											
g. <i>Cinclus mexicanus unicolor</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x		

TABLE 7 Continued

	Oregon coast	Humboldt	Sanoma	Mann	Santa Cruz	Monterey	Trinity	Cascades	Warner	Santa Nevada	Mount Pin.	San Bernardino	San Jacinto	San Diego mountains	Sierra San Pedro Martir	Inyo mountains
38. <i>Troglodytes troglodytes pacificus</i>	x	x	x	x	x	x				x						
<i>Thryomanes bewickii marinensis</i>	(R)	x	(x)	x												
h. <i>Turdus migratorius propinquus</i>	x	x	x	x	x	x	x	x	x	x		x				x
39. <i>Icterus naevius naevius</i>	x	x														
<i>Hylocichla guttata slevini</i>		(x)	x	x	x	x	x	x								
40. <i>Hylocichla guttata sequoiensis</i>								x	x	(x)	x	x				
<i>Hylocichla guttata polymota</i>																(x)
<i>Hylocichla ustulata almae</i>																
41. <i>Hylocichla ustulata ustulata</i>	x	x	x	x	x	x	x	x	x	x		x				
<i>Sialia mexicana bairdi</i>																
42. <i>Sialia currucoides</i>							x	x	x	x		x				
43. <i>Myadestes townsendi</i>							x	x	x	x	x	x	x			
44. <i>Regulus satrapa olivaceus</i>	x	x	x	x	x		x	x	x	x	x	x	x			
45. <i>Regulus calendula cinereus</i>							x	x	x	x	x	x	x			
46. <i>Bombicilla cedrorum</i>	x	x														
47. <i>Vireo solitarius cassinii</i>							x	x	x	x	x	x	x			
<i>Vermivora celata orestera</i>									x							
48. <i>Vermivora ruficapilla ridgwayi</i>							x	x	x	x						
49. <i>Vermivora virginiae</i>																
50. <i>Dendroica auduboni auduboni</i>	x	x	x	x	x	x	x	x	x	x	x	x	x			
[<i>Dendroica townsendi</i>]		x														
51. <i>Dendroica occidentalis</i>	x	x					x	x		(x)						
52. <i>Oporornis tolmiei tolmiei</i>	x	x	x	x	x	x	x	x	x	x						
53. <i>Wilsonia pusilla pilosella</i>																
54. <i>Wilsonia pusilla chrysola</i>	x	x	x	x	x	x	x	x		x	x	x	x	x		
<i>Agelaius phoeniceus caurinus</i>	(x)	x														
55. <i>Piranga ludoviciana</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
56. <i>Heperiphona vesperina brooksi</i>		x					x	x	x							
57. <i>Carpodacus purpureus californicus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
58. <i>Carpodacus cassinii</i>							x	x								
59. <i>Pinicola enucleator californica</i>										(x)						
<i>Leucosticte tephrocotis littoralis</i>								x								
<i>Leucosticte tephrocotis dawsoni</i>										(x)						
60. <i>Spinus pinus pinus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x			
<i>Loxia curvirostra sitchensis</i>		x	x													
61. <i>Loxia curvirostra bendirei</i>							x									
<i>Loxia curvirostra grinnelli</i>										(x)	x	x	x			
62. <i>Chlorura chlorura</i>									x	x	x	x	x			
<i>Passerculus sandwichensis brooksi</i>	(x)	x								x	x	x	x			
63. <i>Junco oreganus thurberi</i>	(R)	x	x	x			x	x	x	(x)	x	x	x	x		
<i>Junco oreganus pinosus</i>						(x)										
64. <i>Junco caniceps caniceps</i>																
<i>Zonotrichia leucophrys oriantha</i>								x	x	x						
65. <i>Zonotrichia leucophrys pugetensis</i>	(x)	x														
<i>Zonotrichia leucophrys nuttalli</i>			x	x	(x)	x										

TABLE 7-- Concluded

	Oregon coast	Humboldt	Sonoma	Marin	Santa Cruz	Monterey	Trinity	Cascade	Warner	Sierra Nevada	Mount Pinos	San Bernardino	San Jacinto	San Diegan mountains	Sierra San Pedro Mártir	Inyo mountains
66. { <i>Passerella iliaca fulva</i>									(x)							
<i>Passerella iliaca megarhynchus</i>							x	x		(x)						
<i>Passerella iliaca brevicauda</i>							(x)									
<i>Passerella iliaca monoensis</i> . . .										(x)						
<i>Passerella iliaca canescens</i> . . .																(x)
<i>Passerella iliaca stephensi</i> . . .										x	x	(x)	x			
67. <i>Melospiza lincolni alticola</i> . . .						x	x	x		(x)		x	x			
<i>Melospiza melodia cleonensis</i> . .	x	(x)														
Total boreal species	33	31	23	21	19	20	47	55	44	54	35	36	31	15	11	28
(Total for California, 67)																
Total boreal species and wide-spread boreal races of other species	41	39	31	29	26	26	54	63	51	62	41	42	36	21	17	33
(Total for California, 75)																
Total number of forms	53	53	37	35	29	28	57	67	55	72	42	44	37	22	20	39
(Total for California, 132)																
Number of endemics or differentiates	15	4	2	1	3	4	1	2	1	19	1	4	0	0	6	3

TABLE 8
DIFFERENCE SCORES FOR AVIFAUNAS OF BOREAL GEOGRAPHIC AREAS

Areas compared	Difference score	Type of barrier
Oregon coast—Humboldt	14	2
Humboldt—Sonoma	20	2
Sonoma—Marin	5	1
Marin—Santa Cruz	7	1
Santa Cruz—Monterey	10	1
Humboldt—Trinity	42	2
Sonoma—Trinity	40	2
Trinity—Cascade	20	2
Cascade—Warner	22	1, 2
Cascade—Sierra Nevada	16	2
Sierra Nevada—Mount Pinos	31	1, 2
Mount Pinos—San Bernardino	7	1
San Bernardino—San Jacinto	8	1
San Jacinto—San Diegan mountains	17	1
San Diegan mountains—Sierra San Pedro Mártir	22	1, 2
Sierra Nevada—Inyo mountains	51	1, 2

probably range to near latitude 40° . Only one species shows a racial boundary north of Humboldt Bay, near Trinidad. Therefore the vicinity of latitude 40° seems to be the appropriate place for a line, if it must be a single line, between the Humboldt and Sonoma areas.

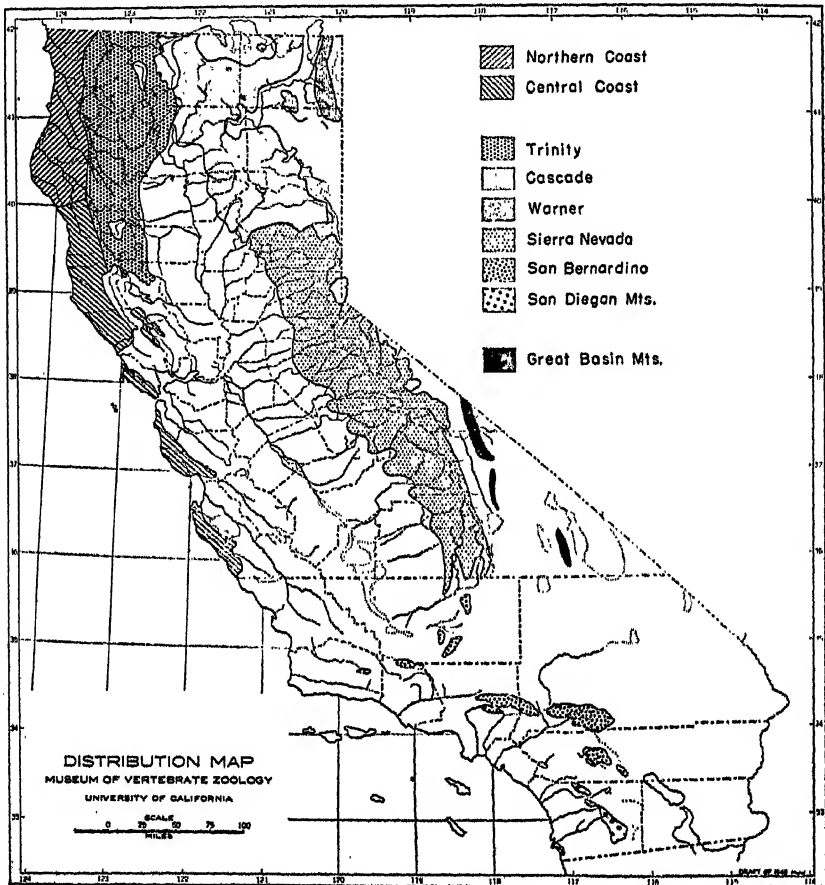


Fig. 3. Boreal faunal districts and areas of California occupied and demarked by different segments of the boreal avifauna. Divisions of Coastal province marked by diagonal lines; Sierran province by various types of dots; Great Basin mountain province by dark tone (see p. 589).

The scores indicating differences between the boreal avifaunas of any two adjoining areas range from 4 to 51 and are fairly evenly distributed over this range but with somewhat sparser representation in the upper values than in the lower ones (see table 8).

The range in scores indicates that several levels of areal and faunal differentiation must be acknowledged in any set of terms used. It is suggested, therefore, that scores of 34 or higher mark faunal provinces; those from 20 to 33, faunal districts; and those from 11 to 19, faunal areas. Scores less than 11 represent minor

areas or subdivisions. Whatever the levels in this hierarchy be called, the units may be arranged to represent the facts by means of an outline, as follows:

- I. Coastal province
 - 1. Northern coastal district
 - a. Oregon coast
 - b. Humboldt
 - 2. Central coastal district (Sonoma, Marin, Santa Cruz, Monterey)
- II. Sierran province
 - 1. Trinity district
 - 2. Sierran-Cascade district
 - a. Cascade
 - b. Sierra Nevada
 - 3. Warner Mountains district
 - 4. Southern Californian mountain district
 - a. San Bernardino (Mount Pinos, San Bernardino, San Jacinto)
 - b. San Diego
 - 5. Sierra San Pedro Mártir district (includes Sierra Juárez)
- III. Great Basin mountain province (= Inyo mountains of California)

The subunits of the boreal avifauna show a general trend of depletion southward on the coast (total boreal species and races dropping from 41 to 26) and in the interior southward from the Sierra Nevada (62 to 17). Depletion southward is not seen in comparing the Cascade, Trinity, Warner, and Sierran units. This apparently is true because the Sierra Nevada compensates for its southern position by a large area of high uplift which affords more high boreal habitats than do the southern Cascade Mountains. The Trinity and Warner boreal faunas are smaller than those of the Cascades and Sierra Nevada principally because of reduction or absence of alpine and subalpine habitats and lack of numbers of lakes and streams at high elevation suitable for boreal water birds.

The difference scores reflect in part the influence of the several areas in the differentiation of distinctive subspecies. However, this aspect alone is not fully revealed by them. For example, *Hylocichla guttata sequoiensis* occurs not only in the Sierra Nevada but in small numbers on Mount Pinos and the San Bernardino Mountains, and as a somewhat modified intergradient type in the southern part of the Cascade area and in the Warner Mountains. It seems fairly clear that the Sierra Nevada is the differentiation center, although this form of thrush is not strictly limited to it. All such subspecies have been reviewed with respect to location of the mass of their populations and the point of extreme development of their characteristics, if known, and are thereupon assigned, when justified, to particular faunal areas as differentiation centers (see table 7). The differentiates attributable to each area are then summated. It is seen that the Oregon coast with 15 differentiates and the Sierra Nevada with 19 are outstanding as differentiation centers. The Sierra San Pedro Mártir with 6 boreal differentiates and the Humboldt, Monterey, and San Bernardino Mountains areas with 4 each and the Santa Cruz and Inyo mountain areas with 3 each rate much lower. Other areas have but 2, 1, or no differentiates.

In the main, these summations seem to stress the factors of a large, fairly well detached land area and distinctive climate, in combination, as underlying causes of differentiation. Detachment seems most important in the Sierra San Pedro

Mártir, whereas distinctive climate seems to be the dominant factor in the two major differentiation centers, the Oregon coast and the Sierra Nevada. Some of the other areas, such as Trinity, even though they are fairly large and their total fauna is fairly distinctive, rate low because they are in reality steps in a gradient between extremes and have little novelty except in the sense of a distinctive combination of elements derived from the extremes. Rather puzzling is the small number of differentiates for the Cascade area. This is partly attributable to the fact that in this analysis we deal only with the southern end of the Cascade area, in the northern part of which are additional distinctive differentiates. It also results probably from the nature of the Cascade system, which is a series of more or less detached high peaks, especially at its southern end. The west-slope fauna of the Oregon Cascades at lower and middle levels is chiefly that of the Oregon coast, from which the mountains are not strongly isolated. Their east-slope fauna bears considerable resemblance to the faunas of the northern Great Basin mountains. In greater degree than the Sierra Nevada the Cascades are a junction area of interior and coastal forms, and in lesser degree they are a unified interior uplift that can develop its own peculiar races.

The boundaries or barriers between the boreal faunal areas seem to fall into two categories, with some of them combining the attributes of these types. First, there are actual discontinuities of coniferous forest environment caused by intervening physiographic or climatic features unfavorable to forest development, and second, there are fairly sharply localized shifts in forest type in a continuous coniferous forest which reflect climatic change or physiographic features, which in turn influence the climate and the biota. Where there is discontinuity, however, there is often, perhaps usually, some degree of this second type of contrast.

In table 8 these two types of barriers, or an obvious combination of them, are indicated opposite the difference scores for each pair of areas. It may be noted that discontinuity alone is associated with low difference scores (5-17). Discontinuity is usually about 20 miles in extent; the few somewhat greater gaps of approximately 40 miles, as between Mount Pinos and San Bernardino (San Gabriel subdivision) do not yield higher scores. The higher indices may or may not be accompanied by discontinuity of forests, but all are associated with conspicuous shifts in the flora reflecting climatic changes. These changes, although often involving temperature, are more obviously related to moisture factors such as rainfall, humidity, and coastal fog blanket.

The most striking changes and some of the highest indices occur between Humboldt and Trinity and between Sonoma and Trinity where there is full continuity of the forests but where interiorly reduced rainfall, increased evaporation rate, and partial blocking of coastal fogs by physiographic features, with consequent altered floral environment, take place over a short distance. The boundary lines between areas here are not as sharp as between discontinuous boreal areas, yet over comparable distances in the forest continuum of 20 to 40 miles much more radical changes take place than across many actual forest gaps.

The discontinuities between Cascade and Warner, Sierra Nevada and Mount Pinos, and Sierra Nevada and the Inyo mountains are certainly accompanied by important climatic and biotic changes, especially noticeable in the last instance,

which also has a very high difference score. The boundaries of Cascade and Sierra Nevada and of Trinity and Cascade, although primarily climatic, are accompanied by actual discontinuities of their high zonal forests if not by breaks in the coniferous forest as a whole.

The over-all picture of differentiation in the boreal environment is one of principal contrast in an east-west direction, with or without forest discontinuity, in broad correlation with strong moisture gradients. This is more striking than the gradual, but nonetheless real, north-to-south depletion phenomenon, which is partly related to temperature differences within the limits of the temperature attributes of the whole boreal environmental belt.

GREAT BASIN AVIFAUNA

The Great Basin avifauna is composed chiefly of Great Basin and Great Plains species. Only a few of its members pertain especially to the far eastern part of the continent. The fauna is found chiefly in areas below the coniferous forest belt, in terrestrial formations such as grassland, sagebrush, pifion-juniper, and riparian woodland and in the aquatic and semiaquatic environments. The avifauna is concentrated in the area east of the Sierran crest in California and spreads but slightly into the typical Californian woodlands and chaparral of the immediate Pacific drainage. It borders and also interdigitates with the Sonoran intrusive fauna from the southwest and with the Californian endemic element, since these three faunas all are occupants of the nonboreal, or austral, environmental levels. However, the Sonoran avifauna adheres in larger measure than the others to the desert scrub and other formations of the Lower Sonoran areas of the state.

The Great Basin avifauna consists of (1) species of interior continental derivation, south of or below the boreal areas, or at least those currently showing mid-continental or eastern distribution centers, that range into the nonboreal environments of California; and (2) geographic races of Great Basin or mid-continental species, or even of Sonoran, Californian, or Boreal species that as races have differentiated in the Great Basin austral levels or subdivisions thereof along the eastern border of the state.

The total number of species occurring in California which are allocated to the Great Basin avifauna is 35. The total species and widespread races of the Great Basin and Great Plains is 48 for California. In all, 70 forms falling within the foregoing definition of the Great Basin avifauna are considered.

Because the Great Basin, Sonoran, and Californian faunas are extensively intermingled or interdigitated in the state, the same austral geographic units have been delineated for all three, even though some may be insignificantly invaded or occupied by members of one of the avifaunas. Thirteen geographic divisions, accordingly, were examined. A general inspection and trial listing of forms for the units that are fairly obviously set off physiographically and by environmental peculiarities or discontinuities led to a narrowing down of the number to this figure. Boundaries between areas have been determined in accordance with the procedure followed in setting out divisions of the boreal regions of the state (see p. 588). Boundaries here again are frequently compromises or midpoints for the boundaries of several different species in the border zone. The difference scores

TABLE 9
GREAT BASIN AVIFAUNA

	Mojave	Inyo	Shasta Valley	Upper Kern Basin	Sacramento	San Joaquin	San Diego	Mojave	Colorado	Chico Lake	San Inverness	San Benito	Channel Islands
a. <i>Colymbus caspicus californicus</i>	x	x		x		x	x						
1. <i>Aechmophorus occidentalis</i>	x	x			x	x	x		x	x	x		
2. <i>Pelecanus erythrorhynchos</i>	x				x	x			x				
b. <i>Ardea herodias tringanzii</i>													
3. <i>Anas discors</i>	x	x			x			x					
4. <i>Aythya americana</i>	x				x	x	x		x		x	x	
c. <i>Oryzopsis jamaicensis rubida</i>	x	x			x	x	x				x	x	
5. <i>Buteo swainsoni</i>	x	x	x		x	x	x	x				x	
6. <i>Falco mexicanus</i>	x	x	x	x	x	x	x	x	x		x	x	
7. <i>Pedioecetes phasianellus columbianus</i>	x												
8. <i>Centrocerus urophasianus</i>	x	x											
<i>Lophortyx californica canfieldae</i>		(x)											
9. <i>Coturnicops noveboracensis</i>		x											
<i>noveboracensis</i>													
d. <i>Grus canadensis tabida</i>	x												
10. <i>Nannacus americanus</i>	x												
11. <i>Caloptrophorus semipalmatus inornatus</i>	x												
12. <i>Himantopus mexicanus</i>	x	x			x	x	x				x		
13. <i>Recurvirostra americana</i>	x	x			x	x	x				x		
14. <i>Steganopus tricolor</i>	x	x				x							
15. <i>Larus delawarensis</i>	x												
16. <i>Larus californicus</i>	x	x											
d. <i>Chlidonias niger surinamensis</i>	x				x	x						x	
17. <i>Sterna forsteri</i>	x				x	x						x	
<i>Otus asio macfarlanei</i>	x												
<i>Otus asio inyoensis</i>		(x)											
<i>Otus asio cineraceus</i>		x											
f. <i>Bubo virginianus occidentalis</i>	x												
18. <i>Phalaenoptilus nuttallii</i>													
<i>nuttallii</i>	x	x	x					x					
19. <i>Aëronautus saxatalis saxatalis</i>		x		x	x	x	x	x	x		x	x	x
20. <i>Archilochus alexandri</i>	x	x	x	x	x	x	x		x			x	
21. <i>Tyrannus tyrannus</i>	x	x											
22. <i>Sayornis saya saya</i>	x	x		x		x	x	x	x			x	
23. <i>Empidonax griseus</i>	x	x											
<i>Eremophila alpestris lamprochroma</i>	x	x											
g. <i>Petrochelidon pyrrhonota hypopolia</i>		x											
<i>Aphelocoma coerulescens nevadæ</i>		(x)											
24. <i>Pica pica hudsonia</i>	x	x						x					

For symbols used, see table 7.

developed as for the boreal fauna combine data from the three austral faunas. These and the barriers between areas are fully considered in conjunction with the Californian fauna (pp. 598, 602-604).

The subunits of the Great Basin fauna in the several geographic regions show the expected depletion of eastern and Great Basin forms southwestwardly. The greatest number (43) is in the Modoc area, with the Inyo area somewhat lower (35). Across the Sierran-Cascade axis there is an abrupt diminution to 21 and 25 in the Sacramento and San Joaquin valleys, respectively. The annexed areas of limited extent, the Shasta Valley and the Upper Kern Basin, although they actually show a strong affinity with the Great Basin area, are so small in scope that they do not have the ecologic diversity of the larger units; hence, their faunas are impoverished and certain Great Basin types skip over them to reappear in the Central Valley areas. Particularly is this true of water and marsh birds.

Beyond the Central Valley the Great Basin avifauna that persists diminishes less sharply to 19 in the San Diegan area, 11 and 12 in the Mojave and Colorado deserts, and to similar levels in the Coast Ranges and the San Francisco Bay area. Only 5 forms reach beyond to the southern California coastal islands.

The influence of the Modoc and Inyo areas in the differentiation of distinctive subspecies is shown by totals of 4 and 6 forms, respectively. In importance this is equivalent to the differentiation in the Humboldt, Monterey, San Bernardino, and Sierra San Pedro Mártir boreal areas. For both the Modoc and Inyo areas one should acknowledge that the units are not confined to California, but represent actually segments of the Great Basin. The other austral areas in California show no differentiates of the Great Basin fauna, although they include many differentiates of the Californian fauna. The distinction between Modoc and Inyo in total fauna and in differentiates is a major one, owing evidently to climatic differentiation, for there is no discontinuity between them, the connection through western Nevada being complete. The transition is gradual, as is also that between the Inyo and Mojave areas (see also Johnson, Bryant, and Miller, 1948).

The significant barrier westwardly which largely checks the spread of the Great Basin avifauna is the boreal belt of the Cascade-Sierran axis. The Shasta Valley is not thus separated by boreal coniferous timber, for this timber has gaps in it along the Oregon border which permit the westward extension of Great Basin types. However, there is a modification of the Great Basin flora in this valley, and not all Great Basin birds find their normal biotic environments available there; also, there is scant development of aquatic environments. The Shasta Valley itself is barred by boreal environments from the Sacramento Valley austral area, yet there is, or has been, some filtering through this low-boreal timber belt in the vicinity of Mount Shasta. The Shasta Valley thus is an annexed area walled off by barriers from the west-Sierran austral areas but differentiated climatically, although not actually barred, from the Modoc area, so that its general faunal resemblance is somewhat closer to the west Californian than to the Great Basin austral divisions.

The Kern Basin presents a similar situation. The area is connected eastwardly with the Mojave Desert at a point near the southwestern extension of the Inyo area. There is then no real barrier to the east, although the continuities in the

vicinity of Walker Pass are narrow. Westwardly there is no boreal barrier. The oak woodlands do sharply replace the desert scrub formation, so that there are conspicuous changes in austral vegetation, but these woodlands and chaparral are actually a part of this Kern Basin subdivision, with connections north and west along the mountain flanks. They give way to the short grass and atriplex sink country of the southern San Joaquin Valley downslope to the west and northwest. The area is one of rapidly shifting climatic and vegetational conditions without full physiographic or boreal barriers. The fauna as a whole is closer to that of the San Joaquin area than to those to the east. Climatic affinity more than sharp barriers seem to prevail in establishing the character of the adjacent areas north and south of the Sierran uplift.

SONORAN AVIFAUNA

The Sonoran avifauna is composed of desert-dwelling species and those that range into California from the southeast and Mexico in zones no higher than the Upper Sonoran and thus chiefly in desert scrub, arid woodland, riparian woodland, and marsh formations. The birds that are restricted to the chaparral areas in California do not find continuity in this habitat southeastwardly and hence are strongly isolated as endemic races or species in the state, even though they may have had a fairly remote derivation from members of the chaparral or scrub faunas of the Mexican uplands. The Sonoran fauna in California occupies the Colorado and Mojave deserts chiefly, mingling with the other austral faunas in the San Diegan, Inyo, and San Joaquin areas and spreading in small degree to more remote, low-lying areas farther west and north.

The Sonoran avifauna consists, then, of (1) species of southeastern, Sonoran, or arid tropical derivation in areas south of or below the boreal areas, or of those species that at least currently show southeastern or arid neotropical distribution centers which range into the nonboreal environments of California; and (2) geographic races of desert or Sonoran species, or even of Great Basin, Californian, Boreal, or other species that as races have differentiated in the southeastern deserts of the state.

The total number of species occurring in California which are allocated to the Sonoran or southeastern avifauna is 30. The total of Sonoran species and widespread Sonoran or southwestern races is 38. In all, 52 forms falling within the foregoing definition of the Sonoran fauna are considered.

For discussion of the geographic subunits for this fauna see pages 591 and 598 ff. They are the same as those employed for the other austral faunas.

Depletion of the Sonoran avifauna northward is evident even east of the coastal divides as one passes from the Colorado Desert to the Mojave Desert. The total of strictly southeastern or Sonoran species and races drops from 35 to 20, and the total of the Sonoran avifauna from 43 to 26. The Mojave Desert is in fact an area of transition, with extensive mixture of Sonoran and Great Basin faunas. West of the desert rims the Sonoran avifauna (Sonoran species and widespread Sonoran races) drops much lower—to 13 in the connecting Upper Kern Basin, and to 11 and 9 in the San Diegan area and the San Joaquin Valley, respectively. A similar set of facts was derived from a different type of analysis in which the occurrence

TABLE 10
SONORAN AVIFAUNA

	Colorado Desert	Mojave Desert	Inyo	San Diego	Upper Kern Basin	San Joaquin	Sacramento	Mojo	San Francisco	Clear Lake	Channel Islands	San Benito	Shasta Valley
1. <i>Colymbus dominicus bangsi</i>	x												
2. <i>Dendrocygna bicolor helva</i>	x			x		x							
3. <i>Parabuteo unicinctus superior</i>	x												
<i>Oreortyx picta russelli</i>		(x)											
4. <i>Lophortyx gambeli gambeli</i>	x	x											
<i>Rallus longirostris yumanensis</i>	(x)												
5. <i>Zenaidura asiatica mearnsi</i>	x												
6. <i>Columbigallina passerina pallescens</i>	x												
7. <i>Geococcyx californianus</i>	x	x	x	x	x	x	x		x	x		x	
<i>Otus asio yunnanensis</i>	(x)	x											
a. <i>Bubo virginianus pallescens</i>	x	x	x										
8. <i>Micrathene whitneyi whitneyi</i>	x												
9. <i>Chordeiles acutipennis taczensis</i>	x	x	x	x	x	x	x					x	
<i>Phalaenoptilus nuttallii huoyi</i>	(x)												
10. <i>Calypte costae</i>	x	x	x	x	x	x					x	x	
11. <i>Colaptes chrysoides mearnsi</i>	x												
12. <i>Centurus uropygialis albescens</i>	(x)												
13. <i>Dendrocopos scalaris caetophilus</i>	x	x			x								
14. <i>Tyrannus vociferans vociferans</i>	x	x		x		x						x	
15. <i>Pyrocephalus rubinus flammeus</i>	x	x											
<i>Eremophila alpestris amnophila</i>		x	x		x	x							
<i>Eremophila alpestris leucansiptila</i>	x												
b. <i>Stelgidopteryx ruficollis psammochrous</i>	x			x									
<i>Aphelocoma coerulescens cana</i>		(x)											
<i>Parus inornatus mohavensis</i>	x	x											
16. <i>Auriparus flaviceps acaciurum</i>	x	x											
<i>Psaltiriparus minimus sociabilis</i>		x											
17. <i>Campylorhynchus brunnei-capillus couesi</i>	x	x		x	x								
18. <i>Mimus polyglottos leucopterus</i>	x	x	x	x	x	x	x	x	x		x	x	
19. <i>Toxostoma bendirei</i>	x	x											
20. <i>Toxostoma lecontei lecontei</i>	x	x	x		x	x							
21. { <i>Toxostoma dorsale dorsale</i>	x												
<i>Toxostoma dorsale coloradense</i>	x												
22. <i>Polioptila melanura lucida</i>	x	x											
23. <i>Phainopepla nitens lepida</i>	x	x	x	x	x	x	x					x	
c. <i>Lanius ludovicianus sonoriensis</i>	x												
d. <i>Vireo belli arizonae</i>	x												
24. <i>Vireo vicinior</i>		x		x	x								

For symbols used, see table 7.

TABLE 10 Continued

	Colorado Desert	Mojave Desert	Inyo	San Diego	Upper Kern Basin	San Joaquin	Sanramento	Modoc	San Francisco	Clear Lake	Channel Islands	San Benito	Shasta Valley
25. <i>Vermivora luciae</i>	x												
c. <i>Dendroica aestiva sonorana</i> . . .	x												
<i>Agelaius phoeniceus sonoriensis</i> . .	x												
26. <i>Icterus cucullatus nelsoni</i> . . .	x												
27. <i>Icterus parisorum</i>	x	x	x		x								
f. <i>Molothrus ater obscurus</i>	x	x		x	x	x	x		x	x		x	
g. <i>Piranga rubra cooperi</i>	(x)												
<i>Richmondia cardinalis superba</i> . .	x												
h. <i>Guiraca caerulea interfusa</i>	x												
<i>Pipilo fuscus cremophilus</i>		(x)											
28. <i>Pipilo aberti dumeticolus</i>	(x)												
29. <i>Amphispiza bilineata deserticola</i>	x	x	x		x			x					
30. <i>Spizella atrogularis cura</i>		x	x										
<i>Melospiza melodia suttonis</i>	(x)												
Total Sonoran and arid tropical species	27	18	9	9	12	8	4	2	2	1	2	6	0
(Total for California, 30)													
Total Sonoran species and wide-spread southwestern races	35	20	10	11	13	9	5	2	3	2	2	7	0
(Total for California, 38)													
Total forms	13	27	11	11	13	10	5	4	3	2	2	7	0
(Total for California, 52)													
Number of differentiates	9	6	0	0	0	0	0	0	0	0	0	0	0

of the segment of the Mojave Desert vertebrate fauna found in the Providence Mountains area was traced in coastal and Sonoran districts (see Johnson, Bryant, and Miller, 1948). Extension of the Sonoran avifauna into the more distant coastal areas is very slight except for the San Benito area which borders, and in many respects is similar to, the San Joaquin and San Diegan areas. It is noteworthy that only two Sonoran forms reach the Modoc area and the Channel Islands.

Differentiation of distinctive subspecies which focus in the Colorado and Mojave deserts totals 9 and 6, respectively, a situation comparable to that for the Great Basin avifauna in the Modoc and Inyo areas. It should be noted, however, that 5 of the 6 differentiates of the Mojave Desert are of local occurrence in the desert in Upper Sonoran brush and woodlands. They are in reality isolated differentiates of typically Californian species, not subdivisions of Sonoran species. They show the influence of the Mojave Desert area, but their differentiation is not that of extreme or true low-desert or Sonoran types comparable to a number of differentiates found in the Colorado Desert. Other austral areas in California show no differentiates of the Sonoran fauna. Thus there is no recognized coastal race of the phainopepla, mockingbird, or cactus wren, although such species reach coastal areas.

The separation of the Mojave and Colorado deserts is not a sharp one in most places. The contrast of the two is chiefly in elevation, as along the southwestern escarpment of the Little San Bernardino Mountains and the mountains bordering the Colorado River valley west of Needles. Many penetrations of low desert occur along the southeastern side of the Mojave Desert which provide continuity or near-continuity for the Colorado Desert biota through to the sink bottoms of the Mojave basin.

The physiographic barriers bordering the deserts on the west are not so complete as those along the Sierran-Cascade axis farther north, since a number of passes, such as the Walker, Tejon, Mint Canyon, Cajon, and San Geronio, exist in which there is contact of desert and low-zone coastal floras. However, in these passes, as also along the interspersed mountains, extremely abrupt changes in rainfall and humidity occur. Sharp climatic and correlated biotic barriers therefore are present, and it is at these barriers that many species of birds are checked. (See also discussion of the Kern Basin connection between both desert and Great Basin areas and the San Joaquin Valley, pp. 594-595.)

CALIFORNIAN AVIFAUNA

The Californian avifauna includes a small number of full species (13) of austral environments which as species are essentially confined to the state or, like *Parus inornatus*, seem to have their center there and certainly form the most continuous and dense populations in California. The number of such species is small partly because of the smallness of the area compared with that of the Great Basin and the Sonoran regions. The Californian species, which are chiefly year-around residents, have broken up into many local races. The Californian avifauna includes also a number of west-coast races of other species which as races center in the lower zones in California west of the Sierra Nevada and the deserts. The combination of the extensive racial differentiation of both strictly Californian and other species raises the total of the Californian avifauna in terms of species and subspecies to 104. In this sense the fauna is larger than either that of the Great Basin or of the Sonoran region.

Most of the Californian species and races are presumed to have arisen close to or within their present ranges on the coastal drainages of California. For only a few of the races included in the list, as for example *Columba fasciata monilis* and *Empidonax traillii brewsteri*, is this uncertain and even in these instances it is probable.

The Californian fauna is found principally in the oak woods, riparian woods, and chaparral of the drainages west of the main mountain axis. There is also a rather large proportion of marshland types. There are few that are primarily occupants of grassland.

Thirteen geographic areas for the combined austral faunas (Great Basin, Sonoran, Californian) of the state have been determined in the manner described in connection with the boreal areas; boundary lines have been set in like fashion (fig. 4). The scores indicating differences in the total austral avifauna between adjoining areas are derived as before (see p. 582), but in working from three faunal listings the information from all three had to be carefully combined to avoid

TABLE II
CALIFORNIAN AVIFAUNA

	Char. Lys.	San Jacinto	San Joaquin	San Francisco	San Benito	Kern Basin	San Diego	Channel Islands	Shasta Valley	Modoc	Inyo	Mojave	Colorado
<i>Ardea herodias hyperborea</i> ..	x	x	x	x	x		x	x		x			
<i>Butorides virescens anthonyi</i>	x	x	x	x	x		x		x				x
<i>Trochyruchus calis hesperis</i> ..	x	x	x				x						x
1. <i>Gymnogyps californianus</i>	x*	x*	x	x*	x	x	x						
<i>Buteo lineatus elegans</i> ..	x	x	x	x	x	x	x						
2. { <i>Lophortyx californica californica</i> ..	x	x	x	sp	x	x	x		x	x	sp	x	
<i>Lophortyx californica californica</i> ..								(x)					
<i>Rallus longirostris obsolitus</i> ..				(x)									
<i>Rallus longirostris leucipes</i> ..							(x)						
<i>Litorallus jamaicensis co- turniculus</i>				x			(x)						
<i>Charadrius nivosus nivosus</i>			x	x			(x)						x
<i>Columba fasciata monilia</i> ..	x	x	x	x	x	x	x		x				
<i>Otus asio bendirei</i> ..	(x)			x									
<i>Otus asio quercinus</i>		x	x	x	x	x	(x)			sp	sp	sp	sp
<i>Bubo virginianus pacificus</i> ...	x	x	x	x	x	x	x		x	sp	sp	sp	sp
<i>Phalaenoptilus nuttallii californicus</i>	x	x	x	x	x	x	x		sp	sp	sp	sp	sp
3. <i>Galypte anna</i>	x	x	x	x	x	x	x	x					
4. { <i>Selasphorus samini samini</i>				(x)			x						
<i>Selasphorus samini sedentarius</i>								(x)					
<i>Balanosphyra formicivora</i>													
<i>bairdi</i>	x	x	x	x	x	x	x	x	x				
<i>Dendrocopos pubescens turuli</i>	x	x	x	x	x	x	x		x	x			
5. <i>Dendrocopos nuttallii</i>	x	x	x	x	x	x	x		x				
<i>Sayornis nigricans semialba</i> ...	x	x	x	x	x	x	x	x			x		x
<i>Empidonax traillii brewsteri</i> ...	x	x	x	x	x	x	x		x	x	x		
<i>Eremophila alpestris insularis</i> ..								(x)					
<i>Eremophila alpestris rubra</i> ...		(x)											
<i>Eremophila alpestris actia</i>			x	x	x	sp	x		sp	sp	sp	sp	sp
<i>Aphelocoma coerulescens</i>													
<i>superciliaris</i>	sp	(x)	x			x			x	x	sp	sp	
<i>Aphelocoma coerulescens</i>													
<i>oocleptica</i>				(x)									
<i>Aphelocoma coerulescens californica</i>					(x)		x						
<i>Aphelocoma coerulescens</i>													
<i>obscura</i>							x					x	
<i>Aphelocoma coerulescens insularis</i>								(x)					
6. <i>Pica nuttallii</i>		(x)	(x)		x		x						

For symbols used, see table 7.

* Occurred formerly.

sp. denotes species represented by a race classed with another avifauna. Forms unclassified as to fauna are not thus marked.

TABLE 11 Continued

	Clear Lake	Sacramento	San Joaquin	San Francisco	San Bernardino	Kern County	San Diego	Channel Islands	Santa Val.	Yuma	Inyo	Mojave	Colorado
7. <i>Parus inornatus sequestratus</i>													
<i>Parus inornatus inornatus</i>	x	x	x	x	x								
<i>Parus inornatus kernensis</i>						(x)							
<i>Parus inornatus transpositus</i>							(x)			sp	sp	sp	
8. <i>Psaltiriparus minimus californicus</i>	x	(x)	x			x			x	x			
<i>Psaltiriparus minimus minimus</i>				x	x		x	x			sp	sp	
<i>Sitta carolinensis aculeata</i>	x	x	x	x	x	x	x	x	x				
9. <i>Chamaea fasciata hinshawi</i>	x	x	x		x	x	x		x				
<i>Chamaea fasciata intermedia</i>				(x)									
<i>Thryomanes bewickii spilurus</i>				(x)									
<i>Thryomanes bewickii drymocoelus</i>	x	(x)	x						x				
<i>Thryomanes bewickii correctus</i>					x	x	x						
<i>Thryomanes bewickii nesophilus</i>								(x)					
<i>Thryomanes bewickii catuliniae</i>								(x)					
<i>Thryomanes bewickii leucophrys</i>								(x)		sp	sp	sp	
<i>Telmatodytes palustris paludicola</i>							x						
<i>Telmatodytes palustris aestuarinus</i>	x	(x)	x							sp			x
10. <i>Torostoma redidivum sonomae</i>	x	x		x									
<i>Torostoma redidivum redidivum</i>			x		x	x	x					x	
<i>Sialia mexicana occidentalis</i>	x	x	x	x	x	x	x		x	x			
<i>Poliophtila caerulea amoenissima</i>	x	x	x		x	x	x		x		x	x	
<i>Poliophtila melanura californica</i>							(x)					sp	sp
<i>Lanius ludovicianus gambeli</i>	x	x	x	x	x		x		x	x			
<i>Lanius ludovicianus anthonyi</i>								(x)					
<i>Lanius ludovicianus meurnsi</i>						sp		(x)			sp	sp	sp
11. <i>Vireo huttoni huttoni</i>	x	x	x	x	x	x	x	x					
<i>Vireo belli pusillus</i>		x	x		x	x	x				x	x	sp
<i>Vermivora celata sordida</i>							x	(x)					
<i>Dendroica aestiva brewsteri</i>	x	x	x	x	x	x	x		x	x	sp		sp
<i>Geothlypis trichas sinuosa</i>				(x)			x		x	x	sp		sp
<i>Geothlypis trichas chryseola</i>	sp	sp	sp		sp	sp	(x)		sp	sp	sp		x
<i>Agelaius phoeniceus maillardi</i>	x			(x)	x								
<i>Agelaius phoeniceus californicus</i>		(x)	x			(x)							
<i>Agelaius phoeniceus aciculatus</i>						(x)							
<i>Agelaius phoeniceus neutralis</i>							(x)		sp	sp	sp	sp	sp

TABLE 11 Concluded

	Clear Lake	Sacramento	San Joaquin	San Francisco	San Benito	Kern Basin	San Diego	Channel Islands	Shasta Valley	Modoc	Inyo	Mojave	Colorado
12. <i>Agelaius tricolor</i>	x	(x)	x	x	x	x	x			x			
<i>Icterus cucullatus californicus</i>			x	x	x	x	(x)	x				x	x
<i>Icterus bullockii parvus</i>	sp	sp	sp	x	1	sp	x		sp	sp	sp	sp	x
<i>Guiraca caerulea salicinarum</i>		x	x			x	x				x		sp
<i>Carpodacus mexicanus clementis</i>								(x)					
<i>Spinus tristis salicamarum</i>	x	x	x	x	x	x	x		x				
<i>Spinus psaltria hesperophilus</i>	1	x	x	1	x	x	x	x	x	x	x	x	x
13. <i>Spinus lawrencei</i>	1	x	x	x	x	x	x						
<i>Pipilo maculatus fuscicollis</i>	x	(1)	1						x				
<i>Pipilo maculatus fuscifer</i>				(x)	x								
<i>Pipilo maculatus megalonyx</i>						x	(x)						
<i>Pipilo maculatus clementae</i>								(x)		sp	sp	sp	
<i>Pipilo fuscus bullatus</i>									(x)				
<i>Pipilo fuscus carolin.</i>	x	(x)	x			x							
<i>Pipilo fuscus putlans</i>				(1)	x								
<i>Pipilo fuscus crissalis</i>					x		(x)					sp	
<i>Pipilo fuscus sinuatus</i>							x						
<i>Passerculus sandwichensis bryanti</i>				(x)									
<i>Passerculus sandwichensis beldingi</i>						sp	(x)			sp	sp		
<i>Aimophila ruficeps ruficeps</i>	1	1	x	(x)	1	x							
<i>Aimophila ruficeps canescens</i>							(x)						
<i>Aimophila ruficeps obscura</i>								(x)					
<i>Amphispiza belli belli</i>	x	x	1	x	x		x						
<i>Amphispiza belli clementae</i>						sp		(x)		sp	sp		
<i>Spizella atrogularis cana</i>			x			x	x						
<i>Spizella atrogularis aurina</i>				(x)	x					sp	sp		
<i>Melospiza melodia gouldii</i>	x			(x)	x								
<i>Melospiza melodia sumuelis</i>				(x)									
<i>Melospiza melodia pusillula</i>				(x)									
<i>Melospiza melodia maxillaris</i>				(x)									
<i>Melospiza melodia muillardi</i>		(x)											
<i>Melospiza melodia heermanni</i>			(x)			x							
<i>Melospiza melodia cooperi</i>					x		(x)					x	
<i>Melospiza melodia micronyx</i>								(x)					
<i>Melospiza melodia grammia</i>								(x)					
<i>Melospiza melodia clementae</i>								(x)	sp	sp	sp		sp
Total endemic species . . .	11	12	12	12	12	11	13	5	5	4	3	4	0
(Grand total, 13)													
Total number of forms	38	43	46	40	45	37	56	25	22	11	6	8	9
(Grand total, 104)													
Number of local differentiates .	1	5	1	16	1	2	15	17	1	0	0	0	0

duplication of tallying. Occasionally instances arise in which an area with a race of a given species is contrasted with an adjoining area in which two or more races of that species occur. If one of these additional races is of marginal occurrence

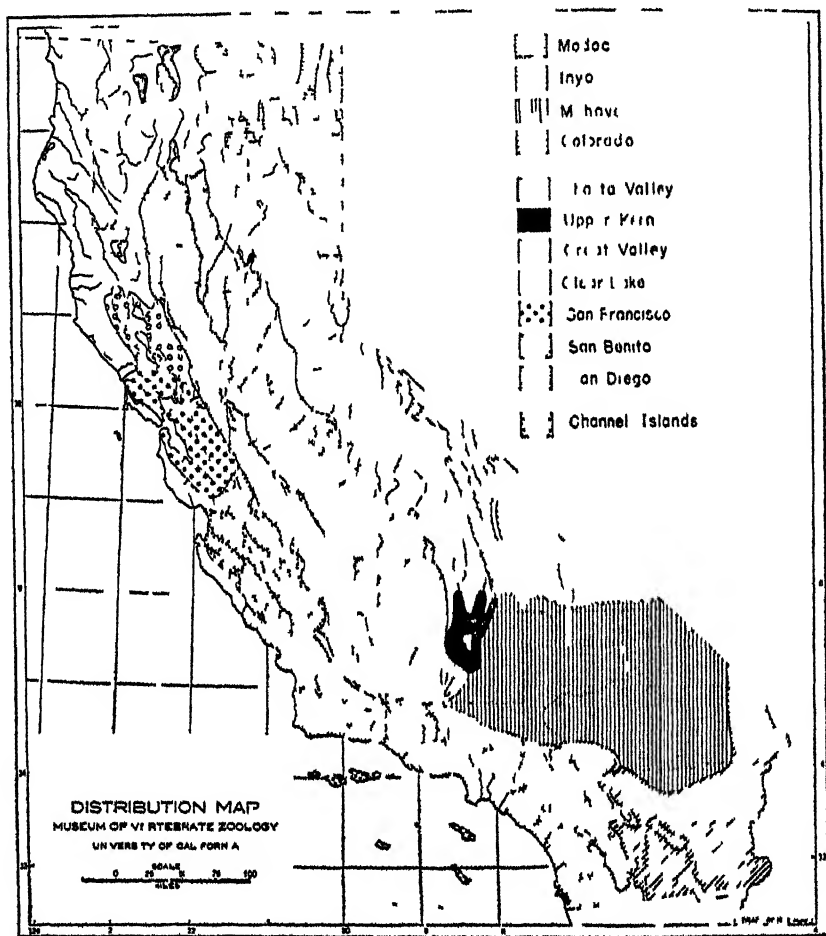


Fig. 4. Austral faunal districts and areas of California occupied and demarked by different segments of the austral avifaunas (Great Basin, Monoran, and Californian). Divisions of Interior province marked by parallel lines; Californian province by various dots and tones, Channel Islands provinces by squares (see p. 604).

in the area concerned, it was disregarded, but if it indicated a measure of additional local differentiation within the area it was counted as a further point of difference. Other special complications had to be adjusted similarly in somewhat subjective fashion in order best to represent the facts. However, the total scores are little altered by these small adjustments and are thought to be reasonably accurate reflections of the degree of difference in the faunas of the areas concerned.

The scores varied from 17 to 77 and were well distributed over this range. The scores are generally much higher than for the subdivisions of the boreal fauna. This situation may be viewed in two ways: (1) the higher values are an absolute reflection of greater differences and hence mark more important subdivisions; or (2) the proportion of difference of the total avifauna involved is of about the same order in the boreal and the austral divisions and, where it is similar, geographic divisions of like importance should be indicated. I am inclined to favor proportional difference, although either position could be defended. Absolute size is one factor

TABLE 12
DIFFERENCE SCORES FOR AVIFAUNAS OF AUSTRAL GEOGRAPHIC AREAS

Areas compared	Difference score	Type of barrier
Modoc—Inyo....	41	2
Inyo—Mojave.....	51	2
Mojave—Colorado...	55	2
Modoc—Shasta.....	50	2
Modoc—Sacramento.....	59	1, 2
Inyo—San Joaquin.....	61	1, 2
Inyo—Kern Basin.....	55	2
Mojave—Kern Basin.....	45	2
Mojave—San Diego.....	72	2
Colorado—San Diego.....	77	2
Shasta Valley—Sacramento.....	35	1, 2
Sacramento—Clear Lake....	23	2
Sacramento—San Francisco....	36	2
Sacramento—San Joaquin....	17	2
Clear Lake—San Francisco....	29	2
San Joaquin—San Francisco....	41	2
San Joaquin—San Benito....	27	2
San Francisco—San Benito....	30	2
San Benito—San Diego.....	31	2
San Joaquin—Kern Basin.....	30	2
San Joaquin—San Diego.....	31	2
Kern Basin—San Diego.....	43	2
San Diego—Channel Islands....	70	1

in recognizing a fundamental difference between the boreal division, with 132 forms, and the austral division, with 226 forms, for it shows a difference in the capacity of the areas and their environments to support species; also, and of course more importantly, the groups of forms in the two are almost completely different. But within each major division there are modifications of essentially one fauna—depletions or differentiations. The degree to which this modification has occurred within a fauna, or the potency of the areas concerned in causing it, is best reflected by the proportion of the total group showing the influence. If two austral areas show a difference score of 25 and two boreal areas the same, the austral areas have been inoperative in producing a difference in 201 members of the fauna, whereas the boreal areas have been without influence on only 106 members.

Consequently, difference scores of boreal and austral divisions would correspond as follows in proportion to the total forms involved in each:

<i>Boreal</i>	<i>Austral</i>
34 or higher	57 or higher
20-33	34-56
11-19	14-33
0-10	0-13

The austral geographic units may be arranged in a system coordinate with that used for the boreal units:

- I. Interior (Great Basin and Sonoran) province
 - 1. Modoc district
 - 2. Inyo district
 - 3. Mojave district
 - 4. Colorado district
- II. Californian province
 - [Annectent areas: Shasta Valley and Upper Kern Basin]
 - a. Great Valley (Sacramento and San Joaquin)
 - b. Clear Lake
 - c. San Francisco Bay
 - d. San Benito
 - e. San Diego
- III. Channel Islands province

The two annectent areas of the foregoing arrangement are somewhat peculiar. Each is comparatively small and does not have the full possible variety of habitats to be found in larger geographic areas (see comments under Great Basin avifauna). Their faunas are accordingly somewhat smaller than those of other areas, the fauna in the Shasta Valley particularly so. The total difference scores separate these annectent areas from the adjacent areas of the Californian province by values barely or not at all sufficient to denote faunal districts. Eastwardly the difference scores are higher, that is, definitely of the value for districts in the system. The Shasta Valley and the Kern Basin thus bridge or break down the high level of difference between the Interior and Californian provinces. The fact that they are but small, semi-isolated areas seems to argue for still recognizing the distinction between Interior and Californian divisions as a major one.

The difference between the avifaunas of the Sacramento Valley and the San Joaquin Valley proves to be so weak that in a system of classification the areas should be merged, just as the Sonoma and Marin boreal areas were merged. Some interesting differences, of course, exist between the bird life of the two valleys, and these should not be lost sight of in the course of placing the total difference in its proper perspective.

The difference scores between the San Francisco Bay region and the Great Valley, either as a unit or in its two parts, are slightly higher than the values set for faunal areas, but it should be noted that the San Benito and Clear Lake areas partly intervene and are faunally intermediate, and that their relations to the San Francisco Bay area are clearly those only of areas, not of districts.

Depletion of the Great Basin and Sonoran avifaunas westward has already been traced. Conversely, the Californian fauna diminishes eastwardly (see totals in table 11).

The composite avifaunas (Great Basin, Sonoran, and Californian) of the austral areas deserve comparison with respect to total size (see table 13). Total number of forms ranges for the most part from 65 to 84. The Shasta Valley has a small total avifauna of 37. The avifaunas of desert areas are somewhat smaller than those of other areas, a reflection of a generally impoverished biota, especially in the Mojave Basin. The total for the Clear Lake area is lower than might be expected, but this is perhaps due to its marginal position toward the boreal regions and its moderate size. The distinctly small island fauna reflects not only the small land mass involved and the reduced number of habitats (especially the lack of marshes) but also the absolute inaccessibility of the area to some species as a consequence of the currently rather wide water barrier. The equivalently small Shasta Valley and Kern Basin areas do not, of course, possess such small avifaunas as do the islands.

TABLE 13
TOTAL AUSTRAL FORMS OF THE GREAT BASIN, SONORAN,
AND CALIFORNIAN FAUNAS

Region	Number	Region	Number
Modoc	69	Sacramento	71
Inyo	70	San Joaquin	84
Mojave	66	Clear Lake	19
Colorado	65	San Francisco	66
Shasta Valley	37	San Benito	68
Kern Basin	69	San Diego	81
		Channel Islands	32

The addition to the totals (table 13) of species unclassified as to fauna, a number of which are water birds, would not greatly alter the relative values of the totals and might obscure the differences in terrestrial conditions which the present totals seem appropriately to indicate.

The localized avian differentiates of the austral areas are totaled in tables 9, 10, and 11, and have been commented upon with respect to the interior districts (pp. 594, 597). The total differentiates for any one interior area range from 4 to 9, values which are equivalent to those for the Humboldt, Monterey, San Bernardino Mountains, and Sierra San Pedro Mártir subdivisions of the boreal fauna. The Californian and Channel Islands areas show higher totals of differentiates in four instances: San Francisco, 16; San Diego, 15; Channel Islands, 17; and Great Valley, 14. The last figure is not readily evident in table 11 and requires explanation; it is derived by combining the totals of the differentiates listed for the San Joaquin and Sacramento valleys, since these areas have been grouped, and adding differentiates that can be attributed to the Great Valley as a whole (marked by two *x*'s enclosed in parentheses in table 11) and those of the Kern Basin, which in a broad sense is but a part of the Great Valley.

In contrast to the areas just listed are those with but one differentiate each: Clear Lake, San Benito, and Shasta Valley. These areas are small or of moderate size and do not have obviously peculiar climatic features, but rather represent stages in a gradient between extremes in adjoining areas.

The four major areas for differentiates—San Francisco, San Diego, Channel Islands, and Great Valley—are on a par with the major boreal differentiation areas, namely, Oregon coast and Sierra Nevada. The interior austral province collectively, that is, considering the total differentiates of its four districts, constitutes another area (or perhaps two—Great Basin and desert) of equal importance in differentiation of distinctive forms of birds.

As with the indices of faunal difference, to which the totals of local differentiates contribute, the most striking contrasts in the differentiation of forms occurs along east-west axes corresponding to a general hygie gradient. Of course there are contrasts north to south, too, among the west-Sierran nonboreal divisions, and indeed not to be overlooked are the very fundamental differences between the boreal and austral faunal categories themselves which align with north-south and altitudinal axes in which temperature is a prominent correlate. Distinctive climates prevailing in large, more or less detached areas seem to be essential attributes of the more effective differentiation centers. This is in a sense a truism, reflecting the widely accepted fact that isolation and the selective action of differing environments both contribute to racial evolution. The instructive aspect of the evidence here under consideration is the differing degree of apparent effectiveness of the areas and the way this correlates with the demarcation of the environments. Detachment is particularly strong for the Channel Islands austral area, but it is weak, whereas climatic contrast is stronger, between the San Diego, San Francisco, and Great Valley areas. The two factors have different weights in the several evolutionary equations, but the end results in number of differentiates may be similar.

Returning to consideration of the whole group of thirteen austral areas tested for distinction by the difference score, we note (table 12) that the type of barrier between areas is usually a climatic-biotic differential, not an absolute discontinuity of the austral environment (see discussion, p. 590). There is less of the latter type of barrier than in the boreal areas which have a more insular pattern of distribution. Only in the Channel Islands-mainland separation and in parts of the Interior-Californian separation is there full discontinuity of austral environments, and this last instance is accompanied by obvious climatic-biotic contrast. Discontinuity alone with respect to boreal areas correlated with *low* differentiation scores. Discontinuity in the Channel Islands area, with a high difference score, is no greater than that between some of the boreal areas in terms of miles, yet the water gap is perhaps more forbidding for the occasional crossing of most terrestrial species than are the uninhabitable lowlands between mountain ranges. Also to be considered is the possibility that we underestimate the climatic difference between the Channel Islands and the nearest mainland; the difference may be as great as that between some of the mainland units west of the Sierra and we may minimize it through preoccupation with the obvious water gap.

In order that the species unclassified in regard to faunas may be noted and the entire group of summer resident birds of California be accounted for, the following list of unclassified forms is appended. It includes chiefly species of marine environments and forms of general continental or holarctic distribution. A further list of forms of widespread western North American distribution, not clearly related with respect to fauna, is added.

<i>Podilymbus podiceps podiceps</i>	<i>Fulica americana americana</i>
<i>Oceanodroma furcata plumbea</i>	<i>Haematopus ostralegus frazari</i>
<i>Oceanodroma leucorhoa beali</i>	<i>Haematopus bachmani</i>
<i>Oceanodroma homochroa</i>	<i>Charadrius vociferus vociferus</i>
<i>Pelecanus occidentalis californicus</i>	<i>Actitis macularia</i>
<i>Phalacrocorax auritus albocollatus</i>	<i>Larus occidentalis occidentalis</i>
<i>Phalacrocorax penicillatus</i>	<i>Larus occidentalis wymanti</i>
<i>Phalacrocorax pelagicus resplendens</i>	<i>Larus atricilla</i>
<i>Osmicrodus albus egretta</i>	<i>Gelochelidon nilotica aranea</i>
<i>Nycticorax nycticorax hoactli</i>	<i>Hydroprogne caspia caspia</i>
<i>Plegadis mexicana</i>	<i>Sterna albifrons browni</i>
<i>Anas platyrhynchos platyrhynchos</i>	<i>Uria aulge californica</i>
<i>Anas cyanoptera cyanoptera</i>	<i>Ceryle alcyon californica</i>
<i>Anas acuta tulaikoa</i>	<i>Brachyrhamphus marmoratus marmoratus</i>
<i>Anas strepera</i>	<i>Endomyschura hypoleuca scrippsii</i>
<i>Spatula clypeata</i>	<i>Ptychoramphus aleuticus aleuticus</i>
<i>Anas sponsa</i>	<i>Certhia monocerata</i>
<i>Aythya collaris</i>	<i>Lunda cirrhata</i>
<i>Elanus leucurus majusculus</i>	<i>Tyto alba pratincola</i>
<i>Accipiter cooperii</i>	<i>Asio wilsonianus</i>
<i>Aquila chrysaetos canadensis</i>	<i>Iridoprocne bicolor</i>
<i>Haliaeetus leucorhynchus leucorhynchus</i>	<i>Riparia riparia riparia</i>
<i>Circus cyaneus hudsonius</i>	<i>Stelgidopteryx ruficollis serripennis</i>
<i>Pandion haliaetus carolinensis</i>	<i>Hirundo rustica erythrogaster</i>
<i>Falco peregrinus anatum</i>	<i>Petrochelidon pyrrhonota pyrrhonota</i>
<i>Falco sparverius sparverius</i>	<i>Progne subis subis</i>
<i>Callus limicola limicola</i>	<i>Vermivora celata lutescens</i>
<i>Porzana carolina</i>	<i>Phaeocephalus melanocephalus maculatus</i>
<i>Gallinula chloropus cachinnans</i>	

GROUP OF GENERAL WESTERN DISTRIBUTION

<i>Leucophrys thula brewsteri</i>	<i>Myiarchus cinerascens cinerascens</i>
<i>Botaurus lentiginosus petti</i>	<i>Corvus corax sinuatus</i>
<i>Cathartes aura litor</i>	<i>Corvus brachyrhynchos hesperis</i>
<i>Buteo jamaicensis calurus</i>	<i>Tragolophus aedon parkmanii</i>
<i>Zenaidura macroura marginella</i>	<i>Vireo gilvus swainsonii</i>
<i>Coccyzus americanus occidentalis</i>	<i>Dendroica nigrescens</i>
<i>Speotyto cunicularia hypugaea</i>	<i>Icteria virens auricollis</i>
<i>Nephocetes niger borealis</i>	<i>Passerina amoena</i>
<i>Megascops alcyon calurus</i>	<i>Geothlypis trichas frontalis</i>
<i>Colaptes cafer collaris</i>	<i>Ammodramus savannarum perpallidus</i>
<i>Tyrannus verticalis</i>	

DISCUSSION

CORRELATION OF ZONAL AND FORMATIONAL RANGES WITH DIFFERENTIATION

The species which show the greatest amount of racial differentiation in California have been examined separately to determine their range of zonal and formational occurrence. As shown in figure 5, the 35 species with 3 or more races breeding in the state have a higher percentage with a zonal range of 3 or more units than does the avifauna as a whole. If the 12 species that are most notably polytypic (5 or more races each) are segregated, we see an even higher proportion with wide zonal range, and few species with a range of 1 or 2. The same general situation prevails in these species with respect to formational range.

The reason for these correlations is not that the species are forming an array of subspecies each peculiar to a single zone or to a single plant formation. The races of birds are not precisely like the ecotypes of plants in which a given ecotype occurs wherever a particular ecologic situation is present within the range of the species. Subspecies of birds are more definitely of geographic aspect, yet their biologically critical attributes are frequently, perhaps usually, related to the zonal or formational attributes of the area they occupy. They are like ecotypes in that they have evolved distinctive characters adapted to ecologic conditions in their range, but the adjustment seems to be related to the average or to a certain range of ecologic conditions and less than in plant ecotypes to a restricted local environmental situation. Probably the movement of individuals and their genes through a bird population is such, in association with moderate selection pressures, that a fluidity is achieved which allows the attributes of the population to level out within

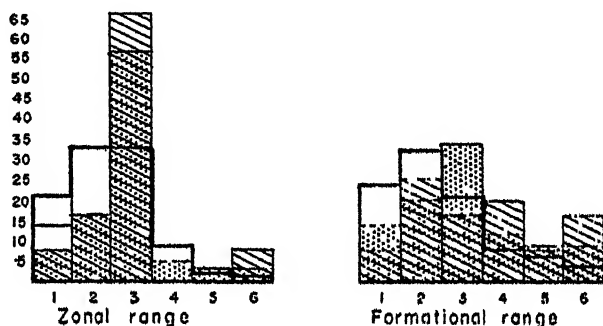


Fig. 5. Frequency occurrence of zonal and formational range in percentage contrasting the breeding avifauna as a whole (outlined by dark line) with polytypic species; polytypic species with 3 or more races breeding in California marked by dots; species with 5 or more races marked by lines.

the barriers of its geographic range and establish gene frequencies fairly uniformly through it which are related to a moderate range of ecologic conditions within the area.

Some examples may be instructive in this connection. Screech owls of the race *Otus asio yumanensis* occur in riparian woodland and desert scrub. The adjoining race *O. a. quercinus* occurs in riparian woodland and in oak woodland. The two races are doubtless adjusted physiologically and instinctively in their foraging and nesting activity on the one hand to cope with desert scrub and, on the other, with oak woods. But the two may occupy in the same way essentially identical types of willow-cottonwood riparian vegetation in their respective geographic ranges. They are not restricted narrowly to one biotic situation, although they may be just as much adapted as are plant ecotypes to two very different ecologic formations, desert scrub and oak woodland, which prevail in their separate geographic spheres.

A thoroughly investigated instance of racial differentiation in correlation with ecologic differences is that in the song sparrows of the San Francisco Bay region (Marshall 1948a, 1948b). In this region the salt-marsh environment supports one type of race (two geographic entities), the upland chaparral, riparian brush, and

fresh-water marsh another type of race. It seems likely that salt-marsh and upland birds possess physiological adaptations to their respective environments, although it is not clear that their external morphological features are thus adaptively related. Each type adheres rather strictly to its own environment, yet in some localities, as at Tomales Bay, the upland type, in the absence of the salt-marsh form, successfully occupies salt marsh. Apparently there is not a rigid ecotypic adherence to the two principal environments, but an important supporting factor of geographic separation leads to ecologic segregation. The most geographically detached salt-marsh populations are the best differentiated, and they apparently would not have developed the degree of divergence (partly ecotypic) that they show without the aiding circumstance of geography.

The races of white-crowned sparrow fall into two zonal categories. The races *Zonotrichia leucophrys pugetensis* and *Z. l. nuttalli* are Transition Zone forms, invading only locally adjoining areas of Upper Sonoran in the coastal fog belt. *Z. l. oriantha* is a Hudsonian-Canadian Zone form of the Sierra Nevada. No race occupies the Transition Zone on the slopes of the interior mountains on which *oriantha* occurs in California, although in Oregon *Z. l. pugetensis* does occur in the foothills. The separation of the two racial types is partly one of geography, even in Oregon. Undoubtedly there is a zonal or environmental adaptation in the races of the species, yet it is an adjustment that has had permissive support from geographic isolation. More strictly zonal races occur in the northern Andes (Chapman, 1917) and other mountains of South America, but this situation is without true counterpart in California.

The situations in *Otus*, *Melospiza*, and *Zonotrichia* which have been cited, and a few other less clear-cut parallels in other genera, come as close to being examples of ecologic or zonal races as are known in western North American birds. It is worth reemphasizing that none has developed this type of differentiation wholly unattended by geographic spacing.

Species that are capable of occupying several zones or formations by reason of adaptability of the individual or because of a good supply of heritable variations in the population are more likely than others to pioneer new geographic and ecologic areas. With geographic isolation aiding, and with some new selective stresses coming to bear that yet do not wipe out the pioneers, a trend toward multiplication of geographic races will occur. This seems to have been true generally in *Melospiza melodia* and in *Passerella iliaca* in California, whereas a close relative of the two, *Melospiza lincolni*, is more rigidly limited, perhaps largely psychologically, as a species to its habitat and has not evolved many races (Miller and McCabe, 1935); only one race occurs in California and the range of the species is narrower in terms of ecologic formations than those of its relatives.

HISTORICAL FACTORS

The avifauna of California has seemed naturally divisible into four units, three intrusive faunas and one endemic fauna. The intrusive faunas, the Boreal, Great Basin, and Sonoran, are broadly continuous with faunas of areas outside the state, and there does not appear to have been any particularly complicated or obscure later ecologic history connected with them. The boreal fauna now occurs disjunctly

in its southern subunits. At one or several times in the Pleistocene there was greater extension of boreal forests southward and down the slopes of the mountains. Beside paleobotanical evidence of boreal biotic extension, there is some evidence from the occurrence of birds themselves in the late Pleistocene. The avifaunas of the Carpinteria asphalt and of some of the Pleistocene caves of northern and central California (Miller, 1937, 1939) indicate that the boreal avifauna extended 200 miles farther south along the coast, at least, and 1,000 feet lower on the interior mountains. Possibly even more extreme extensions occurred in other parts of the Pleistocene. These lines of evidence have a different bearing on the history of each genus and species of bird, but for the boreal fauna as a whole the boreal biotic extension must have meant more continuity of the areas now occupied, with subsequent geographic isolations appearing or being accentuated in the southern half of the state. Doubtless this avifauna disappeared from some southern mountain masses that formerly possessed it. There probably has been, then, an accentuation of the insular aspect of the distributional pattern in the areas now occupied, but the total amount of insularity may not have increased, since peripheral insular areas were lost as new units became detached. That avian differentiates on lost boreal islands moved to other areas as their own areas gradually diminished is unlikely; we would not expect a mass movement but only occasional transfer of an individual. Probably the locally endemic races on boreal islands in the state today are largely products of their present geographic areas and isolations. We see no sure signs to the contrary.

Since the elevation of the Sierra Nevada in the Pliocene, the Great Basin fauna has been fairly sharply excluded from western and central California. Before that time there may have been a broader connection westward, yet I assume that even then some fairly positive climatic differences existed in a west-east gradient and a differentiation of faunas developed in accordance with them to some degree. The lowering of the boreal zones on the Sierra Nevada, together with the height of the mountains, effected a much greater separation of Californian and Great Basin elements in the Pleistocene than now. At present we are probably in a stage of reopening connecting avenues, as in the Shasta and Upper Kern valleys. However, local changes in elevation and in climate in connecting passes may have occurred independently of the general trend, for example in the south, to allow, periodically, even better access than now of the eastern or desert elements to the San Joaquin Valley. The presence of such Sonoran species as LeConte thrashers in this valley (Grinnell, 1933) and the presence in the McKittrick Pleistocene in this valley of the Bendire thrasher, cactus wren, and white-necked raven (Miller, 1937) strongly support this idea.

In the Pleistocene pluvial periods in the Great Basin, the typically Great Basin fauna probably was held to lower levels than now and centered more toward the south. However, its great latitudinal extent today, from southern British Columbia to the Inyo district, suggests that for most of the Pleistocene many of its elements bordered California on the east from Modoc County southward. The conditions of the northern Great Basin of today near the Canadian border may have been those of Modoc County in the Pleistocene, or at least of Nevada to the east of Modoc County, and they may have been much less dominant or widespread there because

of extensive coniferous forests, lake basins, and river bottoms that took up space. But still the Great Basin elements were present, even if reduced in dominance, in areas close to where they occur in California today.

At the southward extreme, on the other hand, we may suppose that the Mojave Desert had the aspect of the Great Basin. Whether the San Joaquin desert fauna of the present and the late Pleistocene arrived in the San Joaquin Valley after the change of the Mojave region to desert aspect or in interpluvial periods of the Pleistocene from small desert remnant populations cannot be decided from data available to me. Certainly we need not assume that the avian desert or Sonoran elements in the San Joaquin Valley arrived there at one time.

The Sonoran avifauna, now broadly continuous northwestwardly into California from Sonora and Arizona, has probably had this connection throughout the Pleistocene. Even though the peninsula of Baja California yields evidence of a previous period of greater rainfall and of greater extension of the northern semixerophilous flora than it now enjoys, it seems likely to me that in the rain shadow of the mountains bordering the Colorado Desert, at least, there were persistent areas of low desert aspect in this period. The extension of elements of this fauna through the passes to coastal southern California and into the Mojave Basin may have been subsequent events. Grassland may have given way to desert scrub in the desert area, but the scrub elements with which the desert avifauna associates were probably there in greater or lesser amount for a long time.

The Pleistocene avifauna of Rancho La Brea of coastal southern California yields little evidence concerning these supposed changes in Sonoran and Lower Californian biotas. The fossils of Rancho La Brea possibly suggest a higher rainfall than now and a more interior type of climatic regime. The last, however, may have resulted from a different configuration of the near-by Santa Monica Mountains (Miller, 1937) and does not necessarily indicate a closer connection than now with the Sonoran areas of southeastern California.

The Californian endemic avifaunal element is found especially in oak woods and chaparral. These floras and the birds that center in them probably were closely associated in their evolution and in California probably date back to the Pliocene. At one time the flora and the avian ancestors, immediate or remote, of the present Californian birds were connected in their distribution with populations in the Mexican plateau. The Madro-Tertiary flora of the Mexican uplands spread into the Rocky Mountains and, via Oregon or Nevada, into California by the Miocene (Axelrod, 1948). Out of a generalized flora, the chaparral, oak woodland, and piñon-juniper elements became specialized, giving rise to the particular chaparrals and woodlands of California that now dominate large parts of the austral areas of the state. With the arrival and differentiation of these floras in middle and late Tertiary, the present Californian endemic birds arrived and differentiated, or they entered into association with the flora by transfer from preëxisting biotas here or elsewhere.

Principal examples of species of birds or their immediate ancestors which probably moved in with the flora are Anna hummingbird, Nuttall woodpecker, plain titmouse, bush-tit, California thrasher, and Hutton vireo. However, among Californian endemics, the yellow-billed magpie probably did not come in in this way

but entered the Californian biota, to differentiate there, from magpie stocks in the Great Basin or northern plains. The wren-tit likewise shows in its present distribution and in its phyletic relationships no signs of having been derived along with the Madro-Tertiary flora, typical and abundant as the species is today in Californian chaparral. The wren-tit's affinities seem to be with Asiatic groups; it could have moved with the understory and border vegetation of the redwood forest, in which it occurs today, around the north Pacific basin, later to spread out in the late Tertiary into the Californian chaparral with which it came in contact.

CLIMATE AND THE MICROEVOLUTION OF BIRDS IN CALIFORNIA

Environmental gradients dictated by climatic factors have been notably effective in inducing racial differentiation and in determining species distribution patterns among the birds of California. This is judged to be true by observing many strong correlations of differentiation and distribution with climatic regions and gradients in the state. The most prevalent sequence of events is thought to be: (1) limitation to particular biotic situations, chiefly to growth forms of plants, by reason of the essential facilities afforded the bird species there; this limitation is often mediated by fairly rigid habitat perception or selection on the part of the bird; (2) subsequent, relatively precise adjustment of a population through natural selection to average, or better, a restricted range of, conditions (background colors, rainfall, insolation, temperature extremes, etc.) within a spatial unit of this biotic type; (3) correlative appearance of clines or step-clines in characters following one or several environmental gradients that run through the geographic subunits of this biotic environment. The distributional pattern of a species as a whole is set primarily by process 1, with historical factors having influence also in determining whether or not all geographic areas of the growth form or biotic type are reached; also some direct action of climatic extremes on the bird may come into play, although usually not if the plant formation, as evinced by its presence, has been able to withstand these extremes. The distributional pattern of races and clines within the species is set partly by minor discontinuities in the biotic environment which may have been hopped at various times by the species, but across which there is no free flow of individuals, and partly by the steepness and irregularities of the climatic, and hence subsidiary, environmental gradients.

Secondary junction of races of one species by reinvasion or range extension after environmentally associated differentiation has occurred, and especially after the origin of some partial or complete intrinsic isolating mechanisms, may lead to a relation of species-like sympatry of the two forms. This occurs infrequently even though it is probably the most usual subsequent step in the transition from race or subspecies to the species. We would not expect that it would be taking place in many genera within the geographic limits of California at any one time. Probable instances of this relation are seen in such species pairs as *Pipilo fuscus* and *Pipilo aberti*, *Dendrocopos scalaris* and *Dendrocopos nuttallii*, *Toxostoma dorsale* and *Toxostoma redivivum*, and *Carpodacus purpureus* and *Carpodacus cassinii*. Members of each of these pairs border or overlap somewhat in range and seem at those junction points to prove their species status adequately by failing to interbreed; yet their distribution and differentiation strongly indicate an antecedent period

as geographic races. On the other hand, *Aphelocoma coerulescens nevadae* and *Aphelocoma coerulescens superciliosa* border and so slightly interbreed in an area of presumed secondary junction that they seem to represent races that almost, yet not quite, attained species status. *Selasphorus rufus* and *Selasphorus sasin* are perhaps beyond, yet certainly are close to, this transitional status; the facts in this case are still very poorly known. *Agelaius tricolor* and *Agelaius phoeniceus* seem to have passed far beyond this stage and are completely sympatric, although an earlier racial status is likely.

We must stress again that underlying this outline of speciation is climatic differential, either directly or indirectly effective, to which all other parts of the mechanism are in a sense auxiliary. There are many facets of climate, but in this survey of presumed events in the development of the avifauna of California one general climatic gradient has become increasingly impressive as a factor directing microevolution. This may be referred to as the hygrogradient—the general change in moisture conditions from a more or less sustained high level of moisture to extreme year-round aridity. It is immediately to be recognized that moisture takes many forms, has important seasonal and annual irregularities, may be measured in a variety of ways, and has a multitude of influences on the animal. Such details need to be examined for each species of bird, but the broad influence of a general hygrogradient is what seems appropriate and possible here to review in relation to the whole avifauna.

The sharpest contrasts of environment and in avian races occur along the breaks in the hygrogradient that occur in the vicinity of the Trinity-Humboldt county line, along the Sierran axis and along the divides between the southern deserts and the coastal plains. (For major climatic types divided along these lines and for detailed data on moisture factors and climate see McAdie, 1914; Russell, 1926; and Trewartha, 1943.) There are, of course, some temperature changes at these same points, but they are not so striking as those of the hygrogradient. To be sure, the thermal gradient latitudinally and especially altitudinally provides some very strong environmental breaks dictating the presence and absence of bird species. (See discussion of contrast of Transition and Upper Sonoran zones, p. 540, and of division of the whole fauna into boreal and austral units, p. 582.) Were more bird species able to range across these points in the thermal gradient, we might find more extensive racial differentiation along this gradient. The species that do thus range widely zonally—and there are many—seldom differentiate racially, however, in close conformance with this temperature gradient (see discussion, pp. 608–609). Contrarily, there is along the hygrogradient a number of points of change so effective that many races give way to their geographic counterparts there. Moreover, as in the temperature gradient, there are species that are limited in their total distribution at such points, for example, *Ictoreus naevius*, *Troglodytes troglodytes*, *Mimus polyglottos*, and *Poliophtila caerulea*.

In a continent-wide survey of distribution, certain broad regularities will be evident that are correlated with temperature because the thermal gradients are basically related to astronomical situations and will have global regularities latitudinally and altitudinally. But in a more restricted area such as California, and particularly in an area along a coastline, the hygrogradient is conspicuous and

rather fully overshadows the effect of the temperature gradient except for the sharp temperature effects associated with mountain systems. The import of the hygrogradient has not been adequately stressed in the past and is seldom appreciated by those who are not familiar with field conditions in California. A similar awareness of the hygrogradient is desirable along other parts of the Pacific coast; it has indeed come appropriately to attention in Munro and Cowan's (1947) treatment of the birds of British Columbia.

ISOLATION AND MICROEVOLUTION

Although the impress of climate on differentiation among birds is basic, it would be wrong to allow this realization to minimize the role of isolation. So far as we can judge, every ecologically correlated differentiation among the birds of California has been accompanied by spatial separation or allopatry in its early or racial stages. This is a way of saying that all subspeciation is geographic; although environmentally directed, it probably could not have come about without spatial separation as a permissive factor which has retarded gene flow, if no more than through isolation by distance in a continuum. This view, growing out of the detailed inspection of the avifauna of one diversified area, is a substantiation of the general ideas on avian evolution voiced in recent years (see Grinnell, 1928; Miller, 1941; Mayr, 1942). The one situation among the birds of California that has most nearly suggested race formation without allopatry, the subspecies of song sparrows of the San Francisco Bay region, has been shown by Marshall (1948a, 1948b) to be no different from that found in normal geographic subspeciation with isolation; there merely are lesser geographic distances involved than usual.

Isolation by distance has become increasingly appreciated and understood through the demonstration of its potency by Wright (1943) and by efforts to show its applicability to variation in birds (Miller, 1947b). Its occurrence in birds rests on their territorial behavior or at least on their strong tendency, despite potential mobility, to remain fixed geographically in the breeding season. This behavior promotes small effective population size and retards gene flow, and thus, in turn, partial isolation by distance in a continuum. This principle renders understandable the development of minor ecologically correlated differentiates at opposite ends of a single species population of rather wide geographic spread.

Both isolation by distance and isolation of a more sharply drawn geographic type permit random or environmentally unrelated differentiation. Under conditions of strong isolation at least, we can see that such differentiation has appeared, as in the races of song sparrows and loggerhead shrikes on the Channel Islands (Miller, 1947b) and on the mainland in at least one race of red-winged blackbird (*Agelaius phoeniceus aciculatus*) and in the allopatric species of magpie, *Pica nuttallii*. Of course there is always the danger, in thus interpreting the characters of these isolated forms, that we are dealing with the secondary effects of hereditary determiners that regulate other unperceived characters, perhaps physiologic, which are environmentally related.

Race boundaries are characteristically sharp and race units are confined to smaller areas on the average where isolation is strong. In other words, we can perceive insular patterns of races whether or not random differentiation is de-

tected. Such insular patterns are particularly noticeable in the southern boreal areas of California and on the offshore islands. The situation is typified in the distribution of the races of fox sparrows, Bewick wrens, and song sparrows (see Grinnell and Miller, 1944:534, 333, 548, maps). On the mainland at austral levels, larger race areas are more frequent, although not as large as in less diversified continental regions. Still the pattern is that of long, gradual clines with poor boundaries for the few large racial units. As an example, the distribution of the races of the brown-headed cowbird may be cited (Grinnell and Miller, 1944:438).

With respect to barriers involved in isolation, it is necessary to stress that the important consideration is the number of breeding individuals that will transgress the barrier, and not the type of barrier per se. It is conceivable that a resident woodland or chaparral species might move as readily across five miles of water as across five miles of open grassland or dry desert sink. Prevailing winds, severe reduction in food supply, overcrowding, and sight of distant terrain might influence the effectiveness of two different water gaps of equal dimension at any one time. These and many other factors that come differently into play for each species at each barrier constitute the true attributes of the barrier and determine the actual flow of individuals and of genes.

It is, however, worth while to distinguish the following extrinsic isolating situations: (1) isolation by mere distance within a continuous population and occupied habitat; (2) partial retardation of flow in a continuum as a result of possible maladjustment of individuals derived at one extreme to the environment at the opposite extreme; and (3) actual discontinuities in populations of a species—gaps, whether the result of discontinuity of floral formations or of water or land masses. Type 2 is theoretically important but difficult to determine. It is in effect a selection barrier, partial and filterlike, and probably rather weak, operating between races or subraces, or more properly between the individuals typifying them. An apparent case of this type of selective barrier involving adjustment to background colors that has received extensive study is that of the deer mice, *Peromyscus polionotus albifrons* and *P. p. polionotus*, on the Florida coast (Sumner, 1932:75).

Grinnell (1914) places considerable stress on a group of barriers termed intangible: zonal (temperature), faunal (humidity), and associational. These he considers chiefly for their influence in setting the outer boundaries of whole species rather than on movements between segments of the range of a species and in relation to gene flow. This latter emphasis has of course come about subsequently through advances in the study of population genetics. Grinnell's intangible barriers are nonetheless the same factors I have stressed under item 3, as are also his tangible or mechanical barriers. Among the barriers classed by him as intangible, the associational barriers do not now appeal to me as particularly intangible when we envision discontinuities in masses of vegetation of particular growth form to which birds are attached for a variety of reasons. The reasons for attachment may be obscure and complicated and thus "intangible," but the discontinuities of associations are usually rather sharp and obvious, more so than the boundaries of zones or of humidity belts. The temperature and humidity factors can operate occasionally to set precise population limits in space, but usually formational or associational barriers come into play first or coincidentally and

exert the immediate check on the birds' dispersal in the kind of isolation envisioned under type 3.

The temperature and humidity gradients, without often barring avian species as a whole, may, as suggested under situation 2, retard the dispersal of part of the individuals in a population that are not endowed to cope with a given level on the gradient. In this sense these intangible barriers of Grinnell have further meaning, although I am not aware that he considered them operative in just this way.

SUMMARY

Distributional patterns of birds may not be expected to conform to any simple system of major groupings, since the spatial balance of each species is a situation peculiar to that species. The life-zone, biome, and province plans for expressing distributional facts have been used here, with modifications as required, to assort the data on the distribution of the birds of California. No one of these systems constitutes a completely satisfactory master system to which the others may be subordinated, but each expresses or emphasizes certain truths and generalizations, some peculiar to it, some coordinate with certain aspects of the other systems.

Although the temperature characteristics of each life-zone have never been satisfactorily determined, zones or belts of life exist and may be recognized as they follow one another in sequence in accordance with temperature gradients. Zones which are obvious on one mountain face are not readily extended to or equated with those of other distant mountain systems because of differences in other aspects of climate. Some difficulty of this type is encountered even in extending zones from coastal to extreme interior California. The greatest numbers of breeding birds in California occur in the Upper Sonoran and Transition life-zones. Most species have a zonal range of 2 or 3 units; only 21 per cent adhere to a single zone. The contrast between avifaunas of adjoining zones is greatest between Upper Sonoran and Transition; the contrasts between Upper Sonoran and Lower Sonoran and between Transition and Canadian are next in importance. A numerical basis is presented which supports the conclusion that the Canadian, Hudsonian, and Alpine-Arctic zones may be grouped as subzones of a Boreal Zone.

A set of twenty-one ecologic situations, twelve of them terrestrial plant formations, have been selected and defined for purposes of grouping breeding birds. These units are more or less equivalent to the second- or third-order subdivisions of Weaver and Clements' (1938) listing of ecologic formations and are thus in part subdivisions of major biomes; they are somewhat adapted and modified to emphasize aspects of plant growth form more than successional history, the former having particular impact on bird life. The zonal range and the gross areal distribution of each formation are given. Some terrestrial formations correlate well with life-zones, but others range through all or most of the zones. Contrarily, some zones have a narrow range in terms of major formations or biomes, whereas others are associated with many formations.

Species of birds are listed according to ecologic formations on the basis of information on habitat set forth in an earlier report on the Californian avifauna (Grinnell and Miller, 1944). Effort is made to rate the desirability or essentialness of each habitat for each bird species from these qualitative data; the need for

future quantitative work on habitat utilization on a large scale is freely acknowledged.

A score was devised to show the relation of one ecologic formation to another by reason of the number of bird species common to them, lesser weight being given to species common to many formations. The highest scores obtained were those relating fresh-water marsh to lacustrine waters and those relating the three types of coniferous forest to one another. Scores relating the different kinds of scrub formation were low.

The greatest numbers of bird species occur in riparian woodland, montane forest, and oak woodland. The proportion of species showing exclusive or first preference for particular formations was greatest for fresh-water marsh, riparian woodland, and the coniferous forests. Most bird species range through or utilize two or three formations; only 25 per cent adhere to one formation, a situation similar to that for zonal distribution.

Species of restricted zonal range have been compared in regard to formational restriction and vice versa: 16 zonally restricted species have a broad formational range; 25 terrestrial species with a narrow formational range have a broad zonal range. In these species it is important to realize that the less restrictive distributional system, whichever it may be, nonetheless often expresses aspects of range limitation additional to that of the other system. However, more precision in general is registered by the formational system, partly because it is more finely divided as here employed and partly because it reflects climatic factors in addition to temperature; but its greater utility in expressing generalizations is not universally true.

Biotic provinces are dealt with by considering, first, certain partly geographic and partly zonal faunal groupings, namely, Boreal (in the zonal regions above Upper Sonoran), Great Basin, Sonoran, and Californian endemic, the first three being intrusive avifaunas ranging into the state from extensive developments in large areas to the north, east, and southwest, respectively. Within each fauna, geographic subdivisions in either the boreal (Transition and Boreal zones) or austral spheres are compared and tested for significance by matching listings of the faunas for adjoining geographic areas. With this objective test of the distinctiveness of the geographic biotic provinces, different ranks of areal subdivisions could be recognized and coordinated. Thus provinces, districts, and areas are units of decreasing importance, a series of each being recognized under the boreal division (Boreal fauna) and under the austral division (Great Basin, Sonoran, and Californian endemic faunas). The provinces under the boreal division are Coastal, Sierran, and Great Basin mountains. Those under the austral division are Interior, Californian, and Channel Islands. (The faunal districts and areas are listed on pp. 589 and 604.)

Each of the intrusive avifaunas in the state shows depletion of its numbers progressively away from its source outside the state, the more sudden depletions coinciding with various types of barriers, absolute or gradient. The boreal avifauna is the largest, the Sonoran the smallest.

Differentiation of distinctive subspecies is much more pronounced in some biotic areas than in others. The most important centers are the humid or Oregon coast and the Sierra Nevada in the boreal sphere and the San Francisco Bay, San

Diegan, Channel Islands, Great Valley, and Interior (Great Basin and desert) in the austral sphere.

The most striking faunal contrasts and racial differentiations occur along east-west hygrogradients. This situation has not been adequately stressed heretofore in work on the birds of the state. The contrasts may be accentuated by barriers that effect actual discontinuities in populations, but they may occur also in the absence of such barriers. Environmental differences between geographic areas are essential for the development of important faunal differences and for the evolution of racial difference. At the same time, spatial or geographic separation is an invariable adjunct in racial differentiation, even though absolute discontinuity in population is not.

Species of birds that show many racial differentiates have broader zonal and formational ranges as species than do those showing fewer races. The subspecies in such wide-ranging species are not strictly zonal or formational differentiates or ecotypes, but they usually reflect the prevailing range or average of ecologic condition in their exclusive geographic ranges. Species which are capable of occupying several zones or formations by reason of adaptability of the individuals or because of a good supply of heritable variation in their populations are more likely, then, to pioneer new geographic areas and differentiate races in them.

The possible impact of certain major historic events on the avifauna of California is briefly considered. Continuities and discontinuities in the boreal subunits and between the interior and coastal Californian austral units have come and gone with the pluvial periods of the Pleistocene and the consequent lowering or southward extension of the higher zones and the well-watered belts or areas. Probably the locally endemic races on boreal islands in the state today are products of their present or Recent geographic isolation and of the ecologic attributes of the areas involved. Connections between the lowland coastal areas and the Great Basin are probably greater now than during much of the Pleistocene. The Pliocene uplift of the Sierra Nevada contributed to the separation at an even earlier time. The desert faunas, although more restricted geographically in pluvial periods of the Pleistocene than now, have probably carried through from the Tertiary in the extreme southwest in continuity with those of the Sonoran deserts. The Californian endemic avifauna, associated chiefly with chaparral and oak woodland, probably has long been associated with the Madro-Tertiary flora derived from the Mexican highlands, and in the late Tertiary it became isolated in California and variously differentiated from the parent species that originally moved with the flora from the southeast.

Barriers or deterrents to the movements of birds may be divided into three types: (1) isolation by distance within a continuous population, (2) partial retardation of flow in a continuum as a result of selective action on individuals not adapted to the environmental extremes, and (3) actual barriers that effect discontinuity of populations within the species. The associational or floristic barriers included in type 3 are the most immediate in their action, more so than temperature and moisture, in most instances, in causing discontinuities in bird populations. One or several of these types of barriers are essential aids to the microevolution of birds, which fundamentally is a response through natural selection to environmental differences, basically those of climate.

APPENDIX

SYNOPSIS OF CHANGES IN TAXONOMY AND DISTRIBUTION

Departures in nomenclature, taxonomy, and geographic distribution from the compilation of usages and data in Grinnell and Miller's *Distribution of the Birds of California* (1944) are herewith summarized. The changes relate only to the native breeding birds of California which are the subject of the present analysis. The majority of the changes in nomenclature and taxonomy are those advocated by the American Ornithologists' Union Check-list Committee in their reports of the last six years. However, not all changes approved by the committee have been adopted by me.

A. Nomenclatural Changes

- Colymbus nigricollis californicus* becomes *Colymbus caspius californicus*, A.O.U. Comm., 1949: 281.
- Plegadis guarauna* becomes *Plegadis mexicana*, A.O.U. Comm., 1945: 438.
- Branta canadensis canadensis* (part as pertains to California) becomes *Branta canadensis moffitti*, A.O.U. Comm., 1947: 446.
- Anas cyanoptera* becomes *Anas cyanoptera cyanoptera*, A.O.U. Comm., 1944: 444.
- Chaulelasmus* included in *Anas*, A.O.U. Comm., 1946: 429.
- Nyroca* becomes *Aythya*, A.O.U. Comm., 1945: 438.
- Charitonetta* and *Glaucionetta* become *Bucephala*, A.O.U. Comm., 1948: 439.
- Erismatura* becomes *Oxyura*, A.O.U. Comm., 1947: 446.
- Oxyechus* included in *Charadrius*, A.O.U. Comm., 1944: 447.
- Chlidonias nigra* becomes *Chlidonias niger*, A.O.U. Comm., 1948: 440.
- Cepphus columba columba* (part as pertains to California) becomes *Cepphus columba eureka*, Storer, 1950: 28.
- Otus asio gilmani* becomes *Otus asio yumanensis*, Miller and Miller, 1951: 172.
- Micropallas* becomes *Micrathene*, A.O.U. Comm., 1947: 448.
- Cryptoglaux* becomes *Aegolius*, A.O.U. Comm., 1947: 448.
- Chaetura vauxi* becomes *Chaetura vauxi vauxi*, A.O.U. Comm., 1945: 442.
- Geophloeus* becomes *Dryocopus*, A.O.U. Comm., 1947: 449; 1949: 282.
- Dryobates* becomes *Dendrocopos*, A.O.U. Comm., 1947: 449.
- Myiochanes* becomes *Contopus*, A.O.U. Comm., 1947: 450.
- Otocoris* becomes *Eremophila*, A.O.U. Comm., 1947: 450.
- Petrochelidon albifrons* becomes *Petrochelidon pyrrhonota*, A.O.U. Comm., 1944: 452.
- Aphelocoma californica* and *Aphelocoma insularis* included in *Aphelocoma coerulescens*, with vernacular species name of "scrub jay," Pitelka, 1951: 207.
- Aphelocoma californica woodhousei* (part as pertains to California) becomes *Aphelocoma coerulescens nevadae*, Pitelka, 1945: 24.
- Cyanocephalus* becomes *Gymnorhinus*, A.O.U. Comm., 1947: 450.
- Heleodytes* becomes *Campylorhynchus*, A.O.U. Comm., 1947: 451.
- Oporornis tolmiei* becomes *Oporornis tolmiei tolmiei*, Phillips, 1947: 278.
- Hedymeles* becomes *Pheucticus*, A.O.U. Comm., 1946: 432.
- Oberholseria* becomes *Chlorura*, A.O.U. Comm., 1947: 451.
- Pipilo aberti* becomes *Pipilo aberti dumeticolus*, A.O.U. Comm., 1947: 451.

B. Additions to the List of Breeding Birds

- Colymbus dominicus bangsi*, species and race breeds in Colorado River valley, McMurray and Monson, 1947: 125.
- Oreortyx picta russelli*, race endemic in Little San Bernardino Mountains, eastern San Bernardino and Riverside counties, Miller, 1946a: 75.

- Aphelocoma coerulescens caurina*, race recognized in northwest coastal district, Pitelka, 1951: 225.
Aphelocoma coerulescens cana, race endemic on Eagle Mountain, eastern Riverside County, Pitelka, 1951: 237.
Aphelocoma coerulescens obscura, race extends from Baja California into southern California, Pitelka, 1951: 230.
Parus inornatus mohavensis, race endemic in Little San Bernardino Mountains, Miller, 1946a: 76.
Psaltiriparus minimus sociabilis, race endemic in Little San Bernardino Mountains, Miller, 1946a: 78.
Towostoma dorsale coloradense, race recognized in Colorado Desert of Riverside and Imperial counties, van Rossem, 1946a: 80; Johnson, Bryant, and Miller, 1948: 313.
Icterus cucullatus nelsoni, race extends from Arizona into Colorado River valley of California, van Rossem, 1945: 242.
Icterus bullockii parvus, race recognized in coastal districts from San Francisco Bay southward and in Colorado Desert, van Rossem, 1945: 237.
Richmondia cardinalis superba, species and race breeds in Colorado River valley, California, van Rossem, 1946b: 247.
Loxia curvirostra bendirei, race extends from Oregon to breed in Trinity area, A. H. Miller, specimens.
Pipilo fuscus senicula, race extends from Baja California into southern California, J. Davis, MS.

C. Deletions from the List of Breeding Birds

- Sitta carolinensis nelsoni* not regarded as extending into northeastern section, Hawbecker, 1948: 34.
Pipilo fuscus kernensis synonymized with *P. f. carolae*, J. Davis, MS.
Melospiza melodia santaecrucis synonymized with *M. m. gouldii*, Marshall, 1948b: 255.

D. Proposed Changes Rejected

Among the changes proposed since 1944 only the following have been investigated thoroughly enough to justify a definite negative report. Other proposed changes will, if substantiated, have little influence on the analysis of the avifauna here presented.

- Colaptes cafer sedentarius* van Rossem. Race not recognized.
Centurus and *Balanosphyra* not synonyms of *Melanerpes*.
Sayornis saya quiescens Grinnell. A race of Baja California not yet adequately demonstrated to extend to California as a breeding bird; occurs in winter.
Empidonax traillii sopholegus Oberholser. Race not recognized.
Regulus satrapa amoenus van Rossem. Race not recognized.
Oporornis tolmiei intermedia Phillips. Race not recognized.
Geothlypis trichas oregonicola Oberholser. Race not recognized.
Geothlypis trichas californicola Oberholser. Race not recognized.
Geothlypis trichas arizonicola Oberholser. Race not recognized.
Carpodacus cassinii vinifer Duvall. Race not recognized.
Pipilo fuscus wrangeli (Bonaparte). Name not usable for *Pipilo fuscus petulans*, J. Davis, MS.
Melospiza melodia mailliardi Grinnell. Proposal to synonymize with *M. m. heermanni* not accepted.

E. Additional Information on Distribution

Only matters bearing on the type of analysis involved in this paper are cited.

- Isobrychus exilis hesperis*, breeding range extended to Clear Lake, Lake County, A. H. Miller, specimens.
Aythya valisineria, probable breeding along northern border substantiated by records at Tule Lake, Jewett, 1947: 126.

- Mergus merganser americanus*, extension of breeding range on coast to mountains of Monterey County, Miller, 1945: 218.
- Buteo lineatus elegans*, resident in Clear Lake area, Lake County, A. H. Miller, MS.
- Bonasa umbellus sabinii*, extension of breeding range south into central Trinity County, Miller, 1947a: 53.
- Laterallus jamaicensis coturniculus*, breeding in San Francisco Bay area more definitely indicated than formerly, Orr, 1947: 41.
- Calypte anna*, decisive evidence of breeding on Santa Cruz Island, A. H. Miller, specimens.
- Balanosphyra formicivora bairdi*, resident on Santa Cruz Island, Pitelka, 1950:43, A. H. Miller, MS.
- Sayornis nigricans semiatra*, breeding range extended to Imperial Valley, Cardiff, 1950: 166.
- Pyrocephalus rubinus flammeus*, extension of breeding range to Mojave Desert, Jaeger, 1947: 213; Fish, 1950: 137.
- Tachycineta thalassina lepida*, an abnormal zonal breeding station in Colorado River valley, Monson, 1949: 264.
- Aphelocoma coerulescens*, ranges of races revised, Pitelka, 1951: 213.
- Sitta carolinensis*, ranges of races revised, Hawbecker, 1948: 34.
- Telmatoodytes palustris aestuarinus*, breeding range extended to Clear Lake, Lake County, A. H. Miller, specimens.
- Toxostoma redivivum redivivum*, resident of Little San Bernardino Mountains, Riverside and San Bernardino counties, A. H. Miller, specimens.
- Piranga ludoviciana*, summer resident in Marin area, Miller, 1946b: 33.
- Xanthocephalus xanthocephalus*, breeding range extended to Clear Lake, Lake County, A. H. Miller, specimens.
- Molothrus ater obscurus*, breeding range extended to Clear Lake, Lake County, A. H. Miller, specimen.

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PLATES

PLATE 32

a. Desert scrub formation, showing spacing of shrubs and open ground; creosote bush (*Larrea*) is tallest plant in this association. Near Baker, San Bernardino County, in Mojave Desert, Lower Sonoran Life zone. Trilling nighthawks, LeConte thrashers, black-throated sparrows, and house finches are typical inhabitants of area. Photograph taken June 28, 1950, by Alden H. Miller.

b. Sagebrush formation showing height of bushes and alleyways between them; sagebrush (*Artemisia tridentata*) constitutes most of the cover, with scattered bushes of purshia. Government Holes, Providence Mountains, San Bernardino County, in Mojave Desert, Upper Sonoran Life-zone. Poor-wills, Bell sparrows, and Brewer sparrows might be expected to occur in such cover. Photograph taken May 27, 1938, by Elmer C. Aldrich.



a



b

PLATE 5

a Chaparral formation, showing compactness of vegetation and continuity of branchwork, adenostoma association. Cajon Pass, San Bernardino County, in San Diego area. Upper Sonoran Life zone. Western California thrashers, gray vireos, brown towhees, and black chinned sparrows were present in the cover here shown. Photograph taken June 28, 1970 by Alden H. Miller.

b Pinon juniper woodland with intermixture of Joshua trees showing widely spaced trees bare ground and intermixed brush. Some oak shrubs are interspersed with pinons and junipers in this area. Keys View, Joshua Tree National Monument, Riverside County, in Mojave Desert near border of Colorado Desert. Upper Sonoran Life zone. Indigo bunting, woodpeckers, ash throated flycatchers, plum tinamou, and Scott orioles occur here. Photograph taken July 11, 1940 by Robert C. Stebbins.



a



b

a Savanna showing mixture of widely spaced trees and grassland involving valley oaks and cultivated fields not uncommonly trees are even fewer than here shown. Cones near Red Bluff Tehama County Sacramento Valley near margin of Lower and Upper Sonoran life zones. Turkey vultures (shown on dead cottonwood) sharp-shinned hawk mourning doves western larks log-cabin chickadees and larks are common here. Photograph taken April 17 1929 by Joseph Dixon.

b Grassland showing large expanse of mixed grasses and herbs without brush or trees. Los Tiempos Game Refuge Merced County in San Joaquin Valley Lower Sonoran life zone. Burrowing owls horned larks and western meadowlarks occur here. Snow geese shown in picture are winter visitors. Photograph taken February 2 1931 by Alden H. Miller.



a

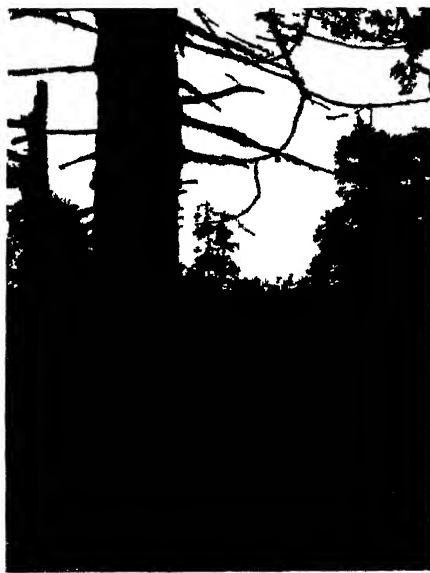


b

PLATE 6

a Alpine meadow bordering Lake below cliffs and talus slopes showing grasses and sedges and clumps of dwarf willows. Vogelzung Lake, Merced County, in Sierra Nevada. Hudsonian and Alpine Arctic life zones. Rosefinches and white-crowned sparrows occur here. Photograph taken August 1, 1915, by Joseph Grinnell.

b c Coastal forest showing density of dominant trees and understory growth. Includes redwood, lowland fir, and tideland spruce, with thimbleberry and fern contributing to the ground cover. Big Lagoon, Humboldt County, in Humboldt area, Transition Life zone. Spotted owls, western flycatchers, Canada jays, chestnut-backed chickadees, winter wrens, varied thrushes, and golden-crowned kinglets occur here. Photographs taken September 21, 1912, by Allen H. Miller.



a Montane forest showing open mature stand of yellow pines with very sparse brush and grass cover on forest floor. West side of Eagle Lake near Spillings, Fresno County. Cascade foothills. Transition life zone. Hairy woodpeckers, white-headed woodpeckers, violet-green swallows, Steller jays, white-breasted nuthatches, and chipping sparrows occur here. Photograph taken October 27, 1921 by Joseph Dixon.

b Subalpine forest showing moderately dense tree clumps about a forest enclosed meadow. Lodgepole pine in field in the conifers shown. Horse Corral Meadow, Fresno County, in Sierra Nevada. Canadian life zone. Calhoun hummingbirds, Williamson sapsuckers, mountain chickadees, hermit thrushes, ruby-crowned kinglets, Audubon warblers, and Oregon juncos are to be found here. Photograph taken September 22, 1916 by Harry S. Swarth.



a



b

PLATE 5

a Inland cliff habitat showing nest and refuge places afforded in a steep rock face Cedar Canyon Providence Mountains San Bernardino County in Mojave Desert, Lower Sonoran Life zone Red tailed hawks (nest shown) white throated swifts and canyon wrens utilized this cliff Photograph taken May 22, 1958, by Elmer C Aldrich

b Sea cliff habitat with marine littoral waters and sandy beach in distance sea cliff affords protected nest and roosting sites Near mouth of San Valleys Marin County Transition Life zone Duck hawks western gulls Brandt cormorants (shown in picture at nest) double crested cormorants and herring gulls nest here Photograph taken May 10 1955 by Alden H Miller



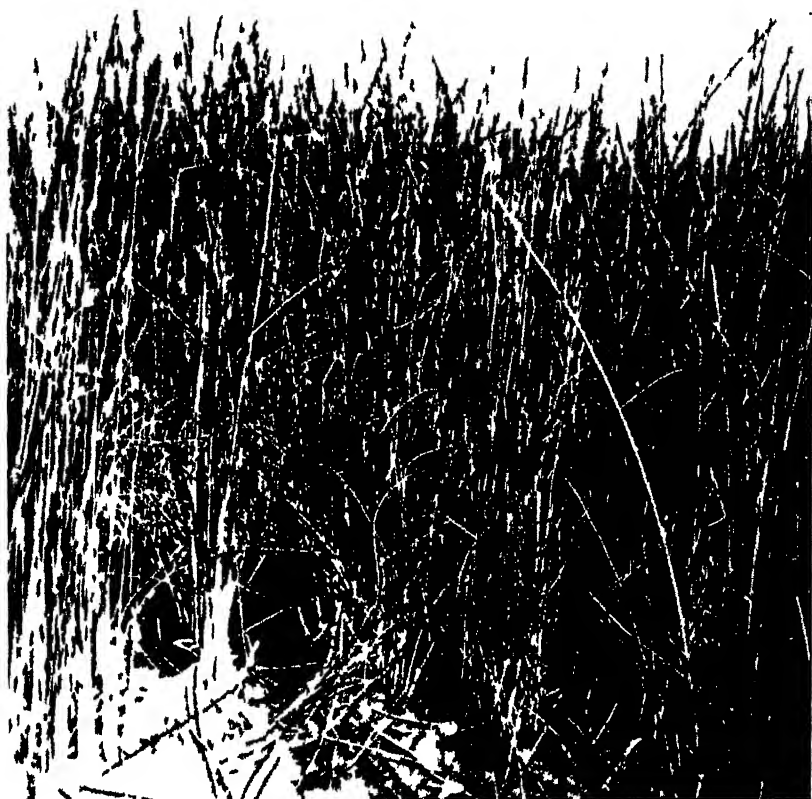
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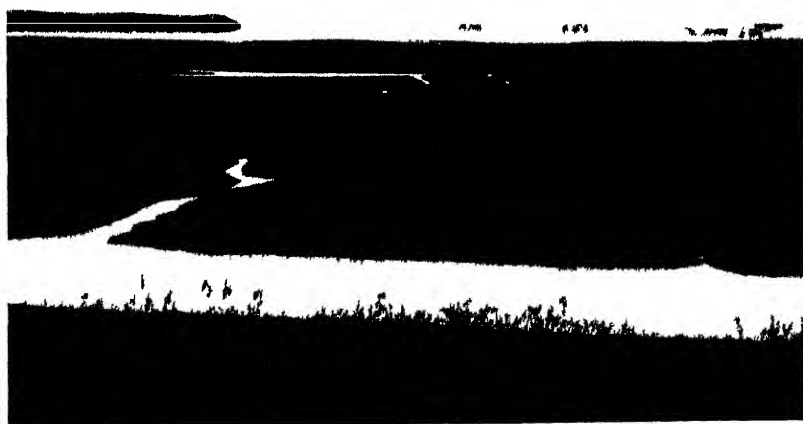
b

a Fresh water marsh, showing water and mud surface with projecting stand of tules. Near Clearlake Park, Lake County, Clear Lake area, Upper Sonoran Life zone. Mallards, Virginia rails, marsh wrens, yellow throats and winged blackbirds, and song sparrows occur here. Photograph taken July 15, 1950, by Alden H. Miller.

b Salt water marsh, showing solid growth of *Salicornia* with tidal channels and slightly exposed mud borders. Morro Bay San Luis Obispo County, San Diego area, Upper Sonoran Life zone. Marsh hawks, cliff swallows, and song sparrows may be expected here. Photograph taken November 7, 1918, by Joseph Dixon.



a



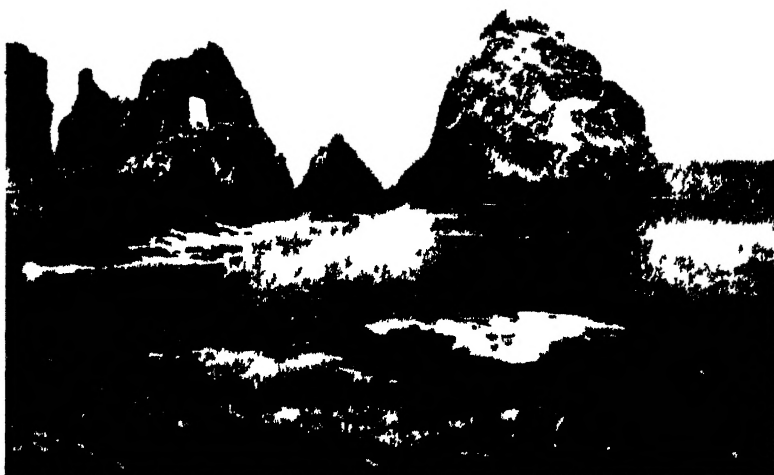
b

a Lacustrine waters with rock and tule borders showing limited wave action Near Clearlake Park, Lake County Clear Lake area Upper Sonoran Life zone Western grebes great blue herons double crested cormorants, ospreys and American coots occur here Photograph taken July 15 1950 by Alden H Miller

b Pelagic and marine littoral waters surrounding tidal rocks essential as nesting sites for pelagic birds, tidal exposure and wave action are indicated South Dillon Island off San Francisco Ashy petrels common murres pigeon guillemots Cassin auklets and tufted puffins nest here Photograph taken April 12 1955 by Alden H Miller



a



b

